GENETICS OF PHOTOPERIOD SENSITIVITY

AND SEASONAL EFFECTS IN CORN (*ZEA MAYS* L.)

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By

Chong Hee Lee

Dissertation Committee:

James L. Brewbaker, Chairman
Henry Y. Nakasone
James C. Gilbert
Douglas J. C. Friend
Duane P. Bartholomew

We certify that we have read this dissertation and that in our opinion it is satisfactory in scope and quality as a dissertation for the degree of Doctor of Philosophy in Horticulture.

DISSERTATION COMMITTEE

James L. Brewbaker
Chairman

Henry Mahasoone

James Gilbert

Douglas J. Fretz

Duane P. Bartholomew

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ABSTRACT

Forty-three corn inbreds were screened for photoperiod insensitivity in controlled growth chambers maintained at 12 and 16 hour daylengths. Tassel initiation determined quantitatively (0.4 mm) was the criterion used in the screening. Photoperiod insensitive and sensitive lines were identified by the above criterion. Tassel elongation of two photoperiod insensitive inbreds (Va35 and Oh43) and two sensitive inbreds (Hi30 and Tx601) under 10, 12, 14 and 16 hour daylengths was logarithmic with time after tassel initiation. No critical daylength was differentiated in this study for corn. Long daylengths delayed tassel initiation resulting in a higher leaf number at the time of tassel initiation for photoperiod sensitive genotypes.

In photoinduction studies, it was found that increasing the number of short days decreased the number of days to tassel initiation and anthesis for photoperiod sensitive genotypes. Conversely, increasing the number of long days increased the number of days to tassel initiation and anthesis for these genotypes. In the hybrid CM104 x Tx601, plants were found to be non-responsive to daylength changes during the first twenty days from planting. Tassel initiation time as well as the period of tassel development were affected by photoperiod, with stronger influence on the former than the latter.

Ten inbreds of differing sensitivity to photoperiod were used to generate a diallel cross. The inbreds were Va35, B37 and Oh43 (insensitive); A619, Hi25 and Hi26 (intermediate); and Hi30, CM104 and Tx601 (sensitive). The inbreds and their 45 F_{1s} were evaluated under normal daylength (average 12.5 hours) and extended daylength of an

additional 4 hours of incandescent light in Hawaii. Days to anthesis and silking were delayed under extended daylength for all genotypes, with sensitive genotypes having the greatest delays and insensitive genotypes having relatively smaller delays. Plant height and ear height were significantly increased under the extended daylength in sensitive genotypes and their crosses with insensitive or intermediate genotypes.

Lower grain yield was observed under extended daylength for genotypes insensitive or intermediate to photoperiod. Cob length was increased although no difference in filled ear length was observed among the insensitive genotypes but was increased among the intermediate genotypes. Both kernels per row and 100 kernel weight were decreased slightly in both group of genotypes. With insensitive x sensitive or intermediate x sensitive crosses, extended daylength increased grain yield, cob length and filled ear length and led to slight increases in kernels per row. Sensitive genotypes showed drastic yield reductions under extended daylength with decreases in cob length, filled ear length, kernels per row, 100 kernel weight and kernel depth. These reductions in yield and yield components were attributed to diseases and poor pollinations, but not daylength effects. Row number on the whole was relatively unaffected by photoperiod. Counts of leaf number and kernel initials per row were increased by long days and with increasing sensitivity to photoperiod of the genotypes.

Days to tassel initiation was found to be highly correlated with days for tassel development, leaf number, days to anthesis and silking. Using only the photoperiod sensitivity, days to tassel initiation was found to have a high correlation with leaf number, days to anthesis and silking.

Photoperiod sensitivity under normal and extended daylength were expressed in days to tassel initiation, days to anthesis, days to silking and leaf number use in the diallel analysis. General combining ability (GCA) and specific combining ability (SCA) mean squares were significant with sensitivity expressed in days to tassel initiation, anthesis and silking. This indicates that both additive and non-additive genes contributed to the genetic variation of photoperiod sensitivity. When leaf number was used, only GCA mean squares were significant. Nevertheless, the GCA/SCA ratio was extremely high in all cases indicating that GCA was more important than SCA. Narrow sense heritability estimates were very high and ranged from 73.9% to 94.7%. In the graphical analysis using photoperiod sensitivity expressed in leaf number, it was found that low sensitivity was partially dominant to high sensitivity, and that photoperiod sensitivity was controlled by a minimum of 2 genes showing some degree of dominance.

Generation mean analysis based on days to anthesis under long days for crosses involving a series of insensitive x sensitive inbreds were carried out. Photoperiod sensitivity and maturity were confounded in this evaluation. Depending on the crosses, additive and/or dominance gene effects were important in controlling days to anthesis with epistasis detected in some crosses. Narrow sense heritability estimates for days to anthesis from the summarized data was 57.43%. The minimum gene number controlling days to anthesis (confounded with photoperiod sensitivity) was on the average 4 (Castle-Wright) or 5 (Sewall Wright) genes with earliness being dominant.

The same set of diallel crosses was evaluated for grain yield and yield components under winter and summer conditions. Planting in winter

reduced grain yield by an average of 54.5% from summer values. Cob length, kernels per row and 100 kernel weight were also reduced in winter as compared to summer. GCA and SCA mean squares for all characters were highly significant in both seasons, with GCA/SCA ratio greater than unity. In the combined analysis, GCA x season and SCA x season mean squares were also highly significant for all the characters studied. GCA/SCA ratios were higher in the winter than in the summer plantings with the exception of kernels per row. The tropical inbreds CM104 and Tx601 showed high combining ability for grain yield under both seasons as compared to the temperate inbreds.

A monthly planting using 6 hybrids was carried out for a period of 20 months. Significant hybrid x months interaction was detected for all characters. Days to mid-silk was earlier in the summer months than in the winter. Plant and ear height, yield and yield components, were generally greater in the summer than in the winter months. The performance somewhat progressed according to the cyclical climatic variations. Plantings in April through August in 1976 were identified as the best months for high grain yield. The best overall hybrid was H763, a temperate by tropical cross.

Multiple regression analyses were also conducted using solar radiation, maximum and minimum temperatures and light duration values as independent variables. Generally, it was found that all the climatic factors studied were important in affecting flowering. Daylength was found to have an important effect on cob length and grain yield. In a separate analysis without using the daylength variable, solar radiation was also found to be important in affecting grain yield. Of the three

months, solar radiation on the third month of the plant's growth, corresponding to grain filling period, was more important than the effects of solar radiation on the earlier two months in contributing to grain yield.

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1. INTRODUCTION

Photoperiod plays an important role in the adaptation of corn by determining the days to flowering (Francis et al., 1969; Francis, 1972c; Hunter et al., 1974; Coligado and Brown, 1975a). The use of tropical materials generally has been restricted to the southern part of the United States or limited to very early and inherently low yielding types such as Zapalote Chico of Mexico (Brown and Goodman, 1977). This is mainly due to its very long vegetative growth period under the temperate daylength conditions.

Sensitivity to photoperiod in corn therefore tends to limit the exchange and use of germplasm among the different latitudes in which corn is grown. Photoperiod insensitive genotypes can be isolated as shown by Francis et al. (1969). The incorporation of photoperiod insensitivity might be valuable to plant breeders in enlarging the source of genetic variability.

In the temperate regions, planting date studies have been conducted to determine the most suitable time of planting for higher grain yield within the limited growing season. In the tropics, corn can be grown throughout the year. Seasonal variations in the climatic factors such as irradiance, temperature, precipitation, wind and humidity have an important effect on the yield performance of corn. Information regarding the effects of seasonal variation on corn yield in the tropics is not known to be available.

It was with these problems in mind that several studies were initiated at the University of Hawaii Agriculture Research Station at Waimanalo. These included the screening of photoperiod insensitive

cultivars and genetic studies on photoperiod sensitivity in corn. This will provide the essential information needed in a breeding program for conversions to low photoperiod sensitivity or insensitivity. Some basic photoperiod response studies in corn were also conducted to provide information for future photoperiod studies of this crop plant. At the same time, a monthly planting of several corn hybrids were carried out to gather information on the effects of some climatic factors on the yield performance of corn. This information will help to make it possible to predict the yielding potential in a given season and may also indicate which hybrid will perform relatively well under varying climatic conditions throughout the year. Such data will also indicate the most suitable time period during which an economical planting of corn can be made.

2. LITERATURE REVIEW

2.1 Inflorescence of Corn

The morphology of the corn inflorescence has been described by a number of workers including Weatherwax (1916, 1917, 1919, 1955), Collins (1919), Arber (1934), Mangelsdorf and Reeves (1939), Sharman (1942), Kiesselbach (1949) and Bonnett (1954). Corn exhibits defined time-patterns in tassel development, and these patterns are heritable (Leng, 1951). Bonnett (1940, 1966) noted that studies of developmental morphology provide useful information on the nature of the variations of some agronomic characters of the corn ear and can help to solve problems of crop production and plant breeding.

2.1.1 Tassel and Ear Initiation

The shoot of the corn plant passes through two distinct phases in the developmental cycle from planting to anthesis (Bonnett, 1940, 1948; Kiesselbach, 1949; Leng, 1951). In the first phase, which is vegetative, leaves and axillary shoots are produced. This phase is terminated with the elongation of the growing point, which marks the beginning of tassel differentiation. The second phase, commencing with tassel initiation, is the period during which the development of reproductive structures occur.

Tassel initiation in corn was considered by Bonnett (1940, 1953, 1954, 1966) to be the stage at which the growing point had elongated and lateral projections or branch initials had arisen acropetally from the growing point of the central axis. Tassel initiation was later defined by Siemer, Leng and Bonnett (1969) as the lengthening of the shoot apical meristem prior to the appearance

of tassel-branch or spikelet primordia. They considered initiation to have occurred when the meristem reached 0.4 mm in length. Tassel initiation marked the end of the period of leaf initial differentiation, that is, the number of leaves would have been determined by this time (Hanway, 1963). At that time the growing point of the stem is at or slightly below the soil surface (Hanway, 1963; Aldrich et al., 1975).

Ear initiation, the beginning of ear differentiation, is indicated by an elongation of the growing point of the axillary shoot and according to Bonnett (1940, 1966) has occurred when lateral projections from the central axis of the ear initials have been differentiated. Siemer, Leng and Bonnett (1969) defined ear initiation as the lengthening of the axillary meristem prior to the appearance of spikelet-forming branch primordia. They considered this to have occurred when a length of 0.5 mm was reached.

In wheat, barley and rye, however, the first definite indication of spike initiation after the elongation of the shoot apex was the appearance of double ridges on the elongated shoot (Bonnett, 1966). A "double ridge" as described in wheat by Friend (1965) is a combination of leaf primordium and spikelet primordium and these double ridges are usually formed first in the central region of the elongating apex, later extending upwards and downwards as the apex continues to elongate.

Days to tassel initiation (DTI) from planting show wide genetic differences in corn (Martin and Hershey, 1934; Kiesselbach, 1949; Leng, 1951; Siemer et al., 1969). In addition, TI time has also been expressed in relation to leaf number (Bonnett, 1940;

Paddick, 1944; Hanway, 1963). Although Leng (1951) reported that there was no correlation between the number of foliage leaves produced and the rate of development, he found that the externally visible leaf number of a genotype gave a fairly good indication of the stage of internal development of the tassel.

In recent studies, Aitken (1971, 1974, 1976) proposed a non-destructive method to estimate the time of tassel or flower initiation as well as to forecast flowering time. The relationship between leaf stage at tassel initiation and the final leaf number was established by using a wide range of genotypes, grown in diverse climates. This relationship was used to predict tassel initiation time by leaf counts at different intervals as well as obtaining a final leaf count. Another method to predict TI time in corn was presented by Coligado and Brown (1975b). This model, the bio-photo-thermal model, involved a genetic factor, mean daily temperature, photoperiod, temperature range and a development potential factor as predictor variables. When tested against the corn-heat-unit, the growing-degree-day, and the U.S. Weather Bureau thermal unit models with and without modifications, they found that their bio-photo-thermal model was superior as predictor of TI time in corn.

There appear to be few publications on days to ear initiation in corn. Bonnett (1954) stated that although tassel development began first, the ear shoot developed rapidly enough so that the silks emerged shortly after the first pollen was shed. Siemer et al. (1969) reported that TI was followed in about 10 days by initiation of the top ear and then of the lower ears.

The vegetative period from planting to TI is influenced by photoperiod and temperature. These effects, which will be treated in more detail in a later section, play important roles in extending the number of days from planting to TI depending on the genotypes. The fact that genetic variation occurred in flower initiation time has been confirmed by Cooper (1956) in a number of grass species. As reviewed by Aitken (1974), drastic leaf removal in the early vegetative stage, as well as low nutrient status of the leaf can retard flower initiation. Although TI was not delayed by higher planting rates (Sass and Loeffel, 1959), it is commonly observed that dense plantings had delayed anthesis and extremely delayed silking.

2.1.2 Tassel and Ear Development

The developmental morphology of both the tassel and the ear in corn have been described by Bonnett (1940, 1953, 1966) and by Kiesselbach (1949). Earley et al. (1974) also presented descriptions and discussions on the ear shoot developmental pattern, the functional relationship between the topmost and the lower ear shoots, and the effects of synthetic growth regulators on the ear shoot development of corn.

After TI, the corn plant undergoes a series of developmental events leading to the emergence of the tassel and the ear shoot, subsequently followed by anthesis, silking, and finally the production of grains on the ear. The time relationship of these events have been outlined by Leng (1951) for the tassel, and by Siemer et al. (1969) for both inflorescences. Leng reported that there was no correlation between the relative earliness of an inbred and the

days to TI. Siemer et al. (1969) concluded from their studies that there were four pairs of events which were closely related in time. These were : (1) tassel initiation and the beginning of stalk elongation, (2) top ear initiation and the beginning of rapid stalk elongation, (3) accelerated tassel peduncle elongation and tassel emergence, and (4) accelerated top ear elongation and attainment of maximum top ear kernels per row potential. Stalk elongation did not occur during the vegetative phase. Immediately after tassel initiation, however, basal internodes begin to elongate. This elongation proceeds from the base towards the tip of the stem (Bonnett, 1954).

The development of potential ears in a corn plant was investigated by Collins (1963). According to him, visible axillary buds developed acropetally in all the leaf axils except the top 6 or 7 before tassel initiation. However, during the stage of rapid development of the tassel, there was a drastic suppression of growth of all the axillary buds. This apical dominance was expressed by the tassel. Rapid elongation of the top ear shoots began only after the growth of the tassel was essentially complete. Collins also reported that prophyll (leaf-like structure associated with the ear) measurements would not be useful in ear developmental studies as he found no correlation between prophyll elongation and cob elongation.

The early stages of tassel and ear development are alike except that there are no branches on normal ears (Collins, 1963). Another similarity in development is their indeterminate growth (Bonnett, 1966). Bonnett (1954) pointed out that the essential morphological difference between the two inflorescences was the

developmental pattern of the basal lateral branches. In the tassel, the basal branches developed into long, unilateral, distichous branches, while in the ear, the basal branches did not elongate, but formed spikelets instead.

2.1.3 Factors Affecting Inflorescence Size

In corn, the development of the ear is basic to grain production and as such any factors affecting plant growth at this stage will be reflected in the final grain yield. The total number of kernels per ear, which constitutes an important yield component, is directly dependent on the total number of fertile florets that the ear will have. Bonnett (1966) stated that the number of fertile florets per spikelet in corn was limited, since only the terminal floret was fertile. The number of spikelets in the ear was then set by the number of spikelet-forming branches, hence pairs of spikelets, and by the number of spikelets per row. Bonnett further pointed out that there was a critical time period when the maximum effect of the growth factors occurred in the ear. Thus, the effective growth with respect to the number of spikelets and florets must take place within this time period.

The length of this ear-development period and floret number, according to Aitken (1966) were genetically controlled. Bonnett (1966), however, indicated that spikelet number potential was not fixed in corn. He stated that indeterminate inflorescences, such as in corn or barley, had the capacity to increase the number of florets by adding spikelets at the tip of the spike, although the maximum number of florets per spikelet was fixed. In the case of

determinate inflorescences, such as in wheat or rye, the number of spikelets could not increase after spike differentiation. Bingham (1967) suggested that extension of this period of critical development of the ear or increasing the rate of ear development before anthesis might be important in increasing yield.

The question of increasing yield through slower inflorescence development was discussed by Aitken (1974). She implied that delayed floral initiation was responsible for increasing the number of spikelets, which in turn, contributed to higher grain yield in winter wheats. She did, however, point out an important problem with regards to slow development and yield. Delayed floral initiation or slow development usually results in late flowering and seed ripening.

The developing inflorescence from the time of flower initiation to flowering is susceptible to the influences of the environment. Considerable evidence has been presented by a number of workers on the effects of temperature, light intensity and photoperiod on inflorescence development of cereals, especially wheat. Friend et al. (1963) showed that in wheat, with increasing temperature between 10° to 30°C or increasing light intensity between 200 to 2500 ft-c, an increased rate of elongation of the developing inflorescence resulted in earlier anthesis. At high light intensities and at low temperatures, Friend (1965) reported that the number of spikelets on the differentiating wheat inflorescence and the head at anthesis was highest. The length of the developing inflorescence and the ear, the height of the main stem, and the total plant dry weight at the time of anthesis were also greatest under these conditions.

Reduction in spikelet number per head was shown by Puckridge (1968) when wheat was grown under dense sowings which was related to the reduction in light intensity caused by self-shading during ear development. Bonaparte (1975) demonstrated that the duration to tassel emergence in corn was slow at low temperatures and under soil fertility and moisture stresses. Temperature affected spikelet number in wheat chiefly by influencing the rate and duration of the appearance of primordia after flower initiation (Halse and Weir, 1974). Warrington et al. (1977) also working on wheat reported that the most important temperature effects were found during the head development phase, and that temperatures prior to floral initiation had little effect on final head weight in the variety they studied. They also found more potentially fertile florets per spikelet at low temperature. Friend (1965, 1966) also stated that long heads with many spikelets were formed at low temperatures because of the long period of slow growth of the developing inflorescence.

Daylength is also known to affect inflorescence development as well as affecting time of floral initiation. Increasing daylength in long day cereals like wheat and barley resulted in faster ear development (Aitken, 1966; Aspinall, 1966; Williams and Williams, 1968) but it was associated with earlier termination of spikelet formation and resulted in smaller heads. It might therefore be possible to obtain large ears in long-day cereals if terminal spikelet formation were to be delayed by shorter daylengths. This was found to be so by Rawson (1970) by growing wheat in short days following long day initiation. As a short-day plant corn would react differently.

Long photoperiod would slow ear development and increase spikelet number. Increased kernel initials per row was demonstrated by Ragland et al. (1966) using supplementary light on corn planted in Kentucky.

The interaction of photoperiod and temperature may also be important in affecting development. Halse and Weir (1974) reported that maximum spikelet number was reached in most of the wheat cultivars they studied at lower temperatures in short days than in longer days.

Intensity of induction also has a pronounced effect on the rate of inflorescence development in both long and short day grasses (Evans, 1964). The more inductive cycles given, and the favorable their daylength, the greater was the subsequent rate of inflorescence development.

Unfavorable environmental conditions during the developmental period of the inflorescence may result in imperfect differentiation of shoot apices (Evans, 1964).

Pistillate spikelets in the tassel or staminate spikelets in the ear are stimulated by short daylengths, low light intensity, lower temperatures, and the imbalance of light and temperature (Schaffner, 1927; Richey and Sprague, 1932; Weatherwax, 1955). Some varieties appeared more amenable than others because of genetic factors such as tassel seed.

2.2 Photoperiodism

The importance of daylength as a major factor in the regulation of flowering time in plants was first realized by Julien Tournois (Vince-Prue, 1975). Garner and Allard (1920, 1923) established convincingly that the different flowering responses in plants were

due to differences in daylength. Recent reviews of this topic include those by Evans (1971) and Zeevaart (1976). In addition, a recent book by Vince-Prue (1975) provides a comprehensive coverage of the photoperiodic responses in plants. The review here deals primarily with corn.

A number of factors have been reported to influence the adaptation of corn. These factors include photoperiod, temperature, intensity of radiation, insects and diseases, soil moisture levels, nutrition and relative humidity (Francis, 1969, 1972b). Photoperiodism per se constitutes a major problem. Garner and Allard (1923) first reported that Peruvian flour corn flowered earlier and attained a much shorter height under short days than long days. Changes in daylength at different latitudes bring about a marked difference in the vegetative growth and flowering time of corn as demonstrated by several earlier workers (Jones and Huntington, 1935; Jenkins, 1941; Kiesselbach, 1950). Although corn is grown widely, there is a limit to its adaptation for corn cultivars from different latitudes. Jenkins (1941) stated that through many generations of selection in different latitudes, corn has become adapted to the length of day in the locality in which they are grown.

2.2.1 Photoperiod Responses

Corn has been classified as a short-day plant as it is sensitive to daylength changes in temperate regions, although it will achieve flowering at any daylength (Garner and Allard, 1938; Jenkins, 1941; Sharman, 1947; Thomas, 1948; Kiesselbach, 1950; Heslop-Harrison, 1961; Arnold, 1969b; Hesketh et al., 1969; Cross, 1971;

Francis, 1972c). The short-day response of corn is quantitative in nature (Moss and Heslo-Harrison, 1968; Hunter et al., 1974). Many cultivars and inbreds are known to show no delay in flowering time under extended daylength i.e. daylength insensitive genotypes (Sprague, 1934; Rogers, 1950; Mes, 1953). Francis (1969, 1970b, 1972a, 1972c) and Francis et al. (1970a, 1970b) reported genotypes which ranged from photoperiod insensitive, i.e. day-neutral, to photoperiod sensitive based on the number of days to tassel initiation under long and short day conditions. Photoperiod sensitivity studies have been carried out by a number of workers using days to TI to set up a sensitivity index, whereas Stevenson and Goodman (1972) utilized leaf number.

Generally, an exchange of corn germplasm between the tropics and the temperate regions brings about unfavorable growth responses. Tropical cultivars flower late and have excessive vegetative growth and taller plants under temperate conditions. Temperate cultivars, however, flower very early resulting in very short plants and low grain yields when they are grown under tropical conditions (Garner and Allard, 1923; McClelland, 1928; Kiesselbach, 1950; Francis, 1970b, 1972a; Francis et al., 1969, 1970b). Delayed flowering and excess leaf production under long day conditions have been attributed to prolonged vegetative growth and delayed tassel initiation (Francis, 1970b; Francis et al., 1970b; Hunter et al., 1974; Coligado and Brown, 1975a; Faungfupong, 1976). There can be a quantitative delay in tassel differentiation and flowering with increasing light intensity of the supplementary light (Francis et al., 1970b; Faungfupong, 1976). Faungfupong (1976) also pointed out that night lighting delayed silking relatively more than tasseling.

Although leaf number increases with increasing photoperiod, there is little or no change in the rate of leaf initiation (Coligado and Brown, 1975a). Spencer (1974) found that plants were taller and had higher leaf number where genotypes showed greater sensitivity to photoperiod. Ear height was also found to increase with increasing daylength (McClelland, 1928; Urano et al., 1959b; Chaudhry, 1968).

Working with C 31 id (indeterminate growth gene) corn, Galinat and Naylor (1951) reported that following photoperiodic induction of this cultivar, tassel proliferation occurred if the photoperiod was greater than 15 hours per day. However, under shorter daylength (11½ and 12½ hour per day) nonfertile flowers in the tassel were produced.

Growing the variety Golden Bantam under a short 8-hour day, Moss and Heslop-Harrison (1968) reported that the plants showed acceleration of tassel and silk emergence, reduced leaf number, fewer tassel branches, smaller number of alicoles (paired spikelets) in the tassel, greatly reduced pollen fertility, and a tendency to sex reversal in the tassel. They assessed fertility on the basis of the numbers of alicoles produced in the inflorescence and the proportion of these showing sterility (or abnormalities). These effects were negated or reduced by night interruption with light at low intensity levels.

Yield components in corn are also affected by changes in daylength. McClelland (1928) was among the first to observe that the number and size of the ears of Porto Rican Corn under extended daylength of 15 hours were inferior to that of normal daylength (which was 11 hours in December and 13.2 hours in June) in Puerto Rico.

In later studies, Ragland et al. (1966) reported that the use of supplementary light in Kentucky (lighting from 11 pm to 3 am in the April planting and from 10 pm to 4 am in the June planting) increased roughly one row number, and also increased the kernels initiated per row in the hybrid C103 x B37. However, there were fewer kernels per row under supplementary light thereby resulting in lower yield. Reduction of grain yield was also observed under night lighting in Iowa by Faungfupong (1976). The mean number of ears per plant was found to increase under long photoperiod whether given as a long day or by night interruptions (Moss and Heslop-Harrison, 1968). However, Faungfupong (1976) observed that supplementary light appeared to have no effect on prolificacy.

Under increasing daylength, Spencer (1974) found that the grain/stover ratios decreased in highly photoperiod sensitive cultivars, but did not affect the photoperiod insensitive cultivars because increased daylength increased both grain and stover yields. Hunter et al. (1977) in growth chamber studies also stated that longer photoperiods produced the highest final plant dry weight in the hybrid, Harrow 691. They attributed this to a higher leaf area per plant which favored higher grain yield.

The vegetative phase of plants are divided into the juvenile phase and the ripeness to flower phase (Vince-Prue, 1975). Juvenility has been defined as the early phase of growth from seed during which flowering cannot be induced by any treatment. The ripeness to flower phase has been described as the situation when the plant will flower in response to the appropriate environmental stimulus. Calder (1966) divided the vegetative phase of grasses into the

juvenile stage, the inductive stage and the stage of realization (initiation). Inductive stage was defined by him as the stage that responds to conditions which promote state of ripeness to flower e.g. cold temperatures and/or short days. Stage of realization (initiation) was described as the stage that responds to conditions which promote inflorescence initiation, chiefly by photoperiod. The plant enters the inductive stage following the juvenile stage. Once the plant is fully induced, it can initiate an inflorescence when grown in an appropriate photoperiod.

Aitken (1977) suggested that the maturity in corn is complex but contains 2 main units, a tendency to flower (strong to weak) and a negative response to long photoperiod (strong to absent) before tassel initiation and that each variety can be ranked on the intensity of each unit. Other units include a response to photoperiod that delays silking more than anthesis, modifiers that affect rates of leaf appearance and seed ripening and also the general responses to temperature common to all varieties.

According to Breuer et al. (1976), the interval between TI and silking was not affected by photoperiod, but was increased significantly by low temperature. However, Aitken (1977) stated that sensitivity to photoperiod in corn delayed not only TI but also silking relative to anthesis.

Francis (1972c) reviewed the reports of several investigators on the determination of the critical daylength for corn. He came to the conclusion that for corn grown in the field, the critical daylength was between 14.5 and 15 hours. He further commented that this would imply that there was never a "long day" in the tropics,

from the physiological or photoperiod standpoint. Hunter et al. (1974), on the other hand, did not observe a critical daylength that differentiated a long-day from a short-day response in their materials, and they suggested a quantitative response to increasing daylength.

In setting up supplementary light for photoperiod studies in corn, it is essential to know the critical light intensity that will cause a photoperiod sensitive reaction. According to Francis et al. (1970b) the magnitude of the delay in tassel differentiation under long day conditions is related to the intensity of light used to lengthen a naturally short day. From their results, they reported that the critical light intensity causing a major delay of floral differentiation was about 54 lux (5 ft-c), with some genetic variation in this response. Light intensities of about 11 to 22 lux (1 to 2 ft-c) would also cause a relatively shorter but significant delay in some sensitive genotypes. However, in some other sensitive genotypes, the lower light intensity did not cause a delay in tassel differentiation. They suggested that there was a separate genetic control of each type of these distinct thresholds of light intensity or delays in floral initiation. Faungfupong (1976) working with the effects of night lighting found that the critical light intensity of a major delay for both tasseling and silking was at about 4 ft-c. Natural photoperiods with a light intensity above the critical level for photoperiod sensitive reactions in plants is greater than the number of sunlight hours, and these are computed for different latitudes to facilitate photoperiod studies in plants (Francis, 1970a, 1972b).

Light quality is another important aspect to consider in supplementary lighting. Incandecent, tungsten, flourescent, and mercury

vapor lamps have been used. White flourescent lamps are commonly used to provide high light intensities required for photosynthesis. However, Friend et al. (1959) reported that they were inferior to incandescent lamps for photoperiodic studies. The high efficiency of the incandescent lamps, according to them, is because of the large part of its energy in the red and far-red regions of the spectrum, which is photoperiodically very effective. On the other hand, the standard cool white flourescent light has a smaller proportion of its energy in the photoperiodically active red and far-red. In fact, most of the workers cited in the preceding sections, have used incandescent lamps for their studies in corn, except Faungfupong (1976) who used mercury vapor lamp.

Not much work has been done on the number of days required for photoinduction of corn. Thomas (1948) reported that shading plants to shorten the daylength for 4 weeks, beginning 4 weeks after seedling emergence, was the most successful of the treatments applied in inducing earlier pollen shed. As reviewed by Vergara and Chang (1976), the number of photoinductive cycles necessary for rice, another short-day plant, increases with the length of the photoperiod. They also observed that Gibberellin A3 reduced the minimum number of photoinductive cycles necessary to induce flowering in rice, although gibberellin alone did not induce flowering under noninductive photoperiods. Since a certain number of photoinductive cycles is required to induce flowering, they suggested that the stimulus produced by the treatment is cumulative and that flower induction takes place when the stimulus has reached a certain threshold level.

Teosinte, a close relative of corn would not flower under continuous long-day (Mangelsdorf, 1974) but would assume a perennial form of growth. Short day treatments were then required to induce them to flower (Emerson, 1924).

2.2.2 Photoperiod and Temperature Interaction

Photoperiod may interact with other environmental factors to affect the development and growth of a plant. According to Evans (1964), daylength usually sets the theme by controlling the time of inflorescence initiation, while variations are played on it by the effects of temperature, light intensity and nutritional status on the rate of development of the initiated inflorescence. Temperature has been known to play an important role in this respect, by modifying the photoperiodic reactions of a number of grasses (Calder, 1966).

Roberts and Struckmeyer (1938) were perhaps the first to detect a photoperiod by temperature interaction in corn. They found no photoperiod sensitivity between 9- and 16-hour daylength with 21^{o}C minimum night temperature, but differences in response were obtained in a cooler greenhouse with 13^{o}C minimum night temperature. In his experiments at different elevations in the tropics, Francis (1972a, 1972c) reported that sensitivity to photoperiod was very small or disappeared under high temperature on the lowlands, but with cooler temperature, there appeared to be an increase in sensitivity. He suggested that lower temperature may allow more time for phytochrome interconversions, and thus a greater expression of sensitivity. High temperature, on the other hand, may accelerate development that there is no time for sensitivity expression. Francis (1972c) also observed that photoperiod had no effect on the growth rate before differentiation, but only on the duration of development from germination to

differentiation. This, according to him, implicated temperature as the main factor which influenced growth rate. Further studies of Hunter et al. (1974), Coligado and Brown (1975a), Schuster et al. (1976), and Breuer et al. (1976) also disclosed that there was a delay in tassel initiation with longer photoperiods at all temperatures but the magnitude of the response was less at high temperature. Conflicting results were obtained by Stevenson and Goodman (1972) who found no loss of sensitivity to photoperiod at high temperature. In fact their results showed that greater sensitivity was observed at high temperature ($34^{o}/30^{o}C$ regimes).

Using different temperatures and photoperiods, Duncan and Hesketh (1968), Hesketh et al. (1969), Hunter et al. (1974, 1977), Coligado and Brown (1975a), and Bonaparte (1975) have reported that leaf number increases with increasing temperature and photoperiod. The length of the grain filling period, i.e. from silking to maturity, is affected principally by temperature, but Breuer et al. (1976) and Hunter et al. (1977) reported the occurrence of photoperiod by temperature interaction. According to their results, corn require more days from silking to maturity under low temperature and long photoperiod. Hunter et al. (1977) also found a significant photoperiod by temperature interaction for kernel number and grain yield as well. Also, they found that the longer photoperiod and cooler temperature treatments produced the highest final plant dry weight.

2.2.3 Genetics of Photoperiod Response

There has been concern among corn breeders in the U.S. of the need to increase genetic diversity in corn after the outbreak of the southern corn leaf blight in 1970 (Lonnquist, 1974; Brown, 1975;

Zuber, 1975). According to Zuber (1975), there has been a large use of 3 inbred lines, A632, Mo17 and B37 and resulting in a narrower germplasm base in the Corn Belt. Exotic corn germplasm can broaden the genetic variability required but most of these materials are from other regions (tropical, subtropical or temperate) and often are not well adapted outside of their environmental range.

Photoperiod has been described as one of the most important factors in the adaptation of corn. The problems associated with sensitivity to photoperiod have been reviewed previously, and to overcome these problems, photoperiod insensitivity must be sought. Francis et al. (1969, 1970b), Francis (1972c) and Spencer (1974) have stressed the importance of isolating photoperiod insensitivity and incorporating it into commercial varieties of corn which can then be easily adapted to the different latitudes in which corn is grown. Cultivars adapted to tropical or subtropical regions are more likely to be photoperiod sensitive, while photoperiod insensitive cultivars may be found in those cultivars adapted to temperate regions (Arnold, 1969b; Spencer, 1974).

Attempts to utilize exotic tropical materials by crossing them with adapted cultivars have been made by several workers including Hallauer and Sears (1972), and Troyer and Brown (1972). Generally, these crosses have been handicapped by lateness due to daylength sensitivity of the tropical germplasm (Lonnquist, 1974). Lonnquist further cautioned that if intensive selection for adaptation is practiced, virtual elimination of the tropical contribution is likely to occur. It is, therefore, of great importance to know the inheritance of insensitivity or sensitivity to photoperiod and the

nature of gene action as this information is a basic requirement to any successful breeding program.

The genetics of photoperiod sensitivity in corn have not been very well established, although there has been some research in this direction. An excessively vegetative plant appeared in a Connecticut sweet corn inbred, C31, and this continuous vegetative growth was attributed by Singleton (1946) to a single recessive gene, id. This mutant remained vegetative under long days and short daylength was required to induce it to flower (Galinat and Naylor, 1951). However, this may or may not be related to the insensitivity "genes" discussed here.

Crosses involving two insensitive varieties were found to be insensitive, while those between sensitive varieties usually were sensitive (Francis, 1972a, 1972c). However, in one cross between two sensitive types D.V.351 x H.207, the F1 was found to be insensitive. The crosses between sensitive and insensitive genotypes were found to be either sensitive or insensitive. Francis (1972a, 1972c) suggested a relatively simple qualitative inheritance based on a small and finite number of genes. Spencer (1974), in his genetic studies also indicated that the response was due to a discrete number of genes showing no or little dominance. In addition he stated that there were indications of possible involvement of modifier genes.

Inheritance studies were also carried out in intergeneric crosses. Langham (1940) reported that a single gene was responsible for the photoperiodic response in crosses between Durango teosinte and corn and that corn was dominant to teosinte for this character. However,

there was no indication of a simple Mendelian ratio in the crosses, Nobogame teosinte x corn and Durango teosinte x corn in the study by Mangelsdorf (1947). In studying the segregating populations of corn-teosinte hybrids, Rogers (1950) reported that several genes are responsible for the photoperiodic response of each of the teosinte varieties.

Flowering in corn has also been used as a criterion in photoperiod response studies. Therefore, genes for photoperiod sensitivity may be related to the genes controlling days to flowering independent of daylength insensitivity. Most of the studies on the inheritance of maturity have used date of anthesis or silking as their basis of maturity. Giesbrecht (1960a) in a brief review reported that the number of genes controlling flowering range from 2 to multiple genes. In his studies, Giesbrecht (1960a, 1960b) suggested that 4 to 5 gene pairs governed flowering time and also indicated the presence of partial phenotypic dominance for earliness and of interallelic interaction of maturity factors. Mohamed (1959) also found that days to silking and days to anthesis were controlled by 3 and 2 major gene pairs respectively in a cross between E.G.102 and E.G.205 with complete phenotypic and genic dominance for earliness. In Hallauer's (1965) studies, he suggested that a maximum of 3 effective factors governed days to silking in a cross between 0h43 (early) and B14 (late) and that additive genetic variation was of major importance.

There have also been great interests in photoperiod insensitivity in the other crop plants. Detailed studies on the inheritance of this character have not been as widespread as the physiology of flowering response. A recent review on the genetic control of flowering

was presented by Murfet (1977) citing a few specific examples including sorghum, wheat, Pisum and Phaseolus.

Studies of the inheritance of photoperiod response in rice (Vergara and Chang, 1976) at the International Rice Research Institute revealed that photoperiod sensitivity was controlled by one (Se) or two (Se_1 and Se_2) dominant genes, while genetic variation in the length of basic vegetative (or juvenile) phase was controlled by 2 or 3 genes (Ef_1, Ef_2,.....) of cumulative but unequal effect. The Se genes were found to be epistatic to the Ef genes under a long photoperiod. They also reported that the short basic vegetative phase was dominant to a long one.

Quinby (1967, 1973) has recently reviewed the genetics of flowering in sorghum. According to him, when sorghum varieties differ in maturity, they do so because they respond differently to photoperiod and temperature. The difference in response was manifested in a difference in time of floral initiation that results in a difference in time of flowering. Four gene loci are now known to control time of floral initiation and duration of growth in sorghum (Quinby and Karper, 1945; Quinby, 1966). These genes segregate independently. Quinby (1973) also stated that they control leaf number and plant size. The 3 maturity loci ma_1, ma_2, ma_3 were first recognized by Quinby and Karper (1945) in the Milo group of varieties. The early genotypes were homozygous for ma_1, with combinations $Ma_1ma_2ma_3$, $Ma_1ma_2Ma_3$, $Ma_1Ma_2ma_3$, and $Ma_1Ma_2Ma_3$ conferring an increasing delay to flowering. Genes Ma_2 and Ma_3 were not expressed in the absence of Ma_1 (Quinby and Karper, 1945, 1961; Murfet, 1977). A third allele at the ma_3 locus (ma_3^R) was later identified from Ryer Milo.

This allele strongly promotes flowering (Quinby and Karper, 1961). In crosses between the Hegari strain and the Milos, transgressive segregation led Quinby (1966) to propose a fourth maturity locus ma_4. It was reported by Quinby (1973) that more than 100 tropical varieties had been converted to temperate zone adaptation by substituting recessive ma_1 for dominant Ma_1. As most tropical varieties are dominant at all four maturity loci, the converted varieties must be of the genotype $ma_1Ma_2Ma_3Ma_4$.

Flowering in sugar cane is undesirable as it reduces the stalk juice and sucrose content. However, there is little or no work done on the genetics of flowering or its photoperiod response, although it has been suggested to be under the control of a complex polygenic system. In a recent study, Lyrene (1977) found that general combining ability was more important than specific combining ability in controlling flowering in sugar cane.

Genetic studies, according to Vergara and Chang (1976), and Murfet (1977) should require adequate separation of the effects in the different phases of growth, and a good control of the interaction of the environmental factors (mainly photoperiod and temperature). Unfortunately, few genetic studies satisfy these requirements.

2.3 Effects of Some Climatic Factors on Corn

Climatic factors affecting corn growth include light, temperature, rain, wind movement, humidity, mist and fog. They interact with one another to produce a complex environmental input for the plant. In this brief review, only the effects of light and temperature will be discussed. Light is important both in duration as well as intensity. The duration

of light or daylength and its effects on the development of corn plants have been previously reviewed.

2.3.1 Light

A corn plant requires abundant sunshine for maximum yields and fails to grow normally in the shade or during extended periods of cloudy weather (Jenkins, 1941). Having the C4 pathway of photosynthesis, rates of CO_2 assimilation by corn increase with increasing irradiance to full sunlight. Pendleton (1968) has stressed that light is the limiting factor in getting higher corn yields, and not water, fertility or carbon dioxide. A similar hypothesis was also put forward by Prine and Schroder (1964) in their "potential yield" studies of corn. There have been numerous studies on the effects of light intensity on corn plants. The main approaches used are shading, use of reflective materials or additional lights, and planting dates.

Shading of corn plants occur naturally under dense plantings due to the reduction of incident light reaching the lower leaves. Increasing plant populations per unit area tend to increase grain yield (Lang et al., 1956; Stickler, 1964; Pendleton, 1965; Colville, 1966; Rutger and Crowder, 1967; Giesbrecht, 1969) simply because of a greater number of plants. However, there is a limit to the beneficial increase in plant populations as demonstrated by several workers. According to Earley (1965), there was a reduction in grain yield per plant, leaf area per plant and leaf efficiency (grams of grain/dm^2 of leaf area). Use of shade treatments have also been carried out. In general, it was observed by Earley et al. (1966) that increased shading throughout the major part of growth brought about a significant decrease in grain yield

and its yield components, while it increased plant height. In addition, the synchronisation between tassel and silk emergence was very much affected. In a later study, Earley et al. (1967) applied shade at the vegetative, reproductive and maturation phases of development. They found that shading during the reproductive phase was the most detrimental of all the three phases in causing significant reductions in grain yield. As reviewed by Bunting and Drennan (1966), studies in the physiology of yield of cereals including corn, rice, wheat and barley have shown that the bulk, if not all, of the dry matter in the grain is produced by assimilation after anthesis.

The importance of light in influencing crop yield can also be demonstrated by supplying the lower leaves of a plant with reflected light from solar radiation or with artificial lights. Using reflective materials, Pendleton et al. (1966) found yield increases in corn when the row interspace was covered with white plastic. White plastic was more effective than black because of its high reflective ratings (80-85% in white and 3% in black). Subsequently, Pendleton et al. (1967) created a "light-rich" environment with large reflectors made of heavy gauge aluminium foil. They reported that in the light-rich environment grain yields were greatly increased, plants had more tillers, there were more plants with two ears, stalks were shorter with greater diameter and plants had a slightly larger leaf area. Graham et al. (1972) also obtained similar results using artificial light directed to leaves from below the ear. Their results suggested that the plants from densely planted corn had not been light-saturated, and thus their potential to photosynthesize had not been fully utilized until the leaves were exposed to a stronger light source.

Date of planting studies in temperate regions usually have the objective of determining the most suitable time at which a crop can be grown with the highest yield. Such studies have been carried out by Grogan et al. (1959), Zuber (1966, 1967), Cardwell (1968), Pendleton and Egli (1969). Early planting in the Corn Belt generally results in higher grain yields. According to Pendleton and Egli (1969), one of the main reasons is that grain formation occurs when the days are longer and the sun is at a steeper angle of incidence and thereby more radiant energy is available for photosynthesis in contrast to late planted corn which matures during the shorter daylengths. This also affects the other agronomic characters. Days to tasseling and silking was greatest for the earliest planting date and decreased with later plantings (Grogan et al., 1959; Zuber, 1966, 1967). Cardwell (1968) working on the response of corn genotypes to planting date and plant population reported that early planting reduced barrenness and increased yields for all hybrids studied. Furthermore, early planting caused high population intolerant hybrids to respond as high population tolerant hybrids.

The relationship of solar radiation to grain yield in corn has also been studied by a few workers. Hatfield et al. (1965) reported that relative yields were reduced as much as 44% when corn was planted late in the normal season and the reduction appeared linear with time after May 1. They found that this reduction in yield was related to the total hours of daylight. Similarly Scarsbrook and Doss (1973) reported that there was a satisfactory fit of their data to a linear regression of grain yield on radiation measured either at 0 or 60 cm above ground. Since grain yield is greatly affected by light, Duncan et al. (1973)

predicted that with other conditions equal, locations with higher insolation would have larger corn yields. In fact, in their location studies, they found that grain yields per hectare were the highest at Davis, which had the highest daily insolation, highest daylight temperatures, and second-lowest night temperatures. Grain yields were lowest at Lexington which had the lowest daily insolation, moderately high daylight temperatures, and the highest night temperatures.

2.3.2 Temperature

Productivity studies on lowland and highland tropical corn by Goldsworthy and Colegrove (1974), and Goldsworthy et al. (1974) indicated that grain yield is limited by the capacity for storage (i.e. grain 'sink') by the plant. However, after anthesis, the major metabolic sinks are the developing grains, and thus the capacity for grain storage will be determined by their number and potential size. The potential for grain storage, then is dependent on the rate and duration of the development of spikelets of the young ear (Goldsworthy, 1974b). As reviewed earlier, low temperature (with high light intensities) resulted in long heads with many spikelets in wheat because of the long period of slow growth of the developing inflorescence (Friend, 1965, 1966), and perhaps also in corn.

The effects of photoperiod and its interaction with temperature have been reviewed previously. In location experiments conducted by Goldsworthy et al. (1974), it was found that silk emergence was delayed by 17 days at two sites and this was related to temperature differences. Moreover, the rate of appearance and expansion of leaves in corn was slower at low temperatures. Thus for a given number of

leaves, anthesis was later at El Baton (2250 m) than at Poza Rica (60 m) (Goldsworthy, 1974a). This delay in flowering by low temperature has been attributed to a delay in tassel initiation time (Coligado and Brown, 1975a) as well as the period from tassel initiation to silking (Breuer et al., 1976). Thus, the corn plant will experience more days of sunlight, and as a result will have more photosynthate for growth, i.e. long duration of dry matter production (Duncan, 1975; Hunter et al., 1977). In addition, prolonged grain filling period occurred under low temperatures (Breuer et al., 1976; Hunter et al., 1977). As a result of this, and also due to the fact that a greater proportion of the post-anthesis dry matter was allocated to the grain, the grain yields were higher at the lower temperature.

Aldrich et al. (1975) stated that respiration loss is excessive when the nights are too warm, thereby resulting in lower yield. However previous work by Semikhatova and Beevers (cited by Duncan et al., 1973) indicated that any effect of temperature on respiration per se would only have a minor effect on the net photosynthate per day available for plant metabolism. In unpublished work at the International Institute of Tropical Agriculture (IITA) under high night temperatures, dry weight loss of corn never exceeded 5% for any night tested (M. Quin, unpublished). Duncan (1975), suggested an alternative explanation. According to him, the important difference is that photosynthesis is governed by leaf temperatures during daylight hours only, whereas development rate is a function of temperature over the whole day. Environments with lower night but similar day temperatures will have slower development rates, whereas higher night temperatures speed

development, decreasing both the number of days of photosynthesis between developmental events and plant dry weight. According to a recent experiment by Peters et al. (1971), large reductions in grain yield resulted from treatments in which plants in the field were kept warmer at night.

Thus, it would be expected that the greatest corn growth would occur in environments conducive to leaf temperatures of 30 - 33°C during the day but with cool nights. Such conditions are characteristic of locations in regions that are arid, or at high elevation. Conversely, warm humid environments at low elevations usually have less diurnal variation and might be expected to produce less total growth (Duncan, 1975).

3. MATERIALS AND METHODS

3.1 Screening for Insensitivity to Photoperiod

Materials chosen for a preliminary screening consisted of 43 inbred lines from tropical as well as temperate regions (Table 1). Two hybrids (H68b, a sweet U.H. hybrid and X306B, a Pioneer Hi-bred International field corn) were also included in the screening. This study was conducted in growth chambers with an inside space of 4 feet by 3 feet and a height of about 3 feet. Each chamber had 20 flourescent lamps (GE F48T12 - CW 1500) and 10 incandescent light bulbs (Westinghouse Standard Bulbs - 60 watts) giving a light intensity of 32,292 lux. Temperature in the growth chambers was set at 26.6°C day and 21.1°C night, while the relative humidity was set at 60%. These temperature conditions were chosen to approximate the average conditions at the Waimanalo Agriculture Research Station. Two chambers were used, in which one was set at 12 hours day and 12 hours night, while the other was set at 16 hours day and 8 hours night. Both flourescent and incandescent lamps were on during the day period.

Twenty seeds of each line were sown in pots (15 cm diameter by 15 cm deep) of sterilized soil. After seedling emergence, they were thinned to 15 seedlings per pot. The pots were watered daily and at later stages of growth twice a day. Fertilizer solution made up of 1 table-spoon of NPK 15-15-15 (approximately 14 gms.) in 1 gallon of water was supplied once in every three days. A seedling from each pot was sampled on alternate days starting on the 8th day after sowing. These were then dissected, and the meristem was measured from the tip to the base of the youngest initiated leaf. When the length of the meristem was

Table 1. Cultivars used for photoperiod insensitivity screening

Cultivars	Source	Cultivars	Source
A619	CB	Oh43	CB
AA8	Trop	Oh545	CB
B37	CB	Tx601	SCB x Trop
B68	CB	Va35	CB
B73	CB	W64A	CB
CI64	SCB	442	Trop
CI66	SCB	74-1610	CB x Trop
CM103	Trop	74-1625-1	CB x Trop
CM104	Trop	74-1629-3	CB x Trop
CM105	Trop	74-1645-4	CB x Trop
CM109	Trop	74-1653-2	CB x Trop
CM111	Trop	74-1665-1	CB x Trop
CM201	Trop	74-1675-2	CB x Trop
F44	SCB	74-1711-1	CB x Trop
Ga209	SCB	74-1721-3	CB x Trop
H95	CB	74-1744-2	CB x Trop
Hi25(B14A)	CB	74-1756-1	CB x Trop
Hi26(CI21E)	SCB	74-1788	CB x Trop
Hi30	Trop	74-1810-2	CB x Trop
Mo17	CB	74-1819-2	CB x Trop
Mp68:616	SCB x Trop	*H68b	Trop
N6G	CB	*X306B	Trop
N28	CB		

Trop - Tropical, CB - Corn Belt (Temperate)
SCB - Southern Corn Belt, * - hybrids

0.4 mm, tassel initiation was considered to have occurred (Siemer et al., 1969).

Differences in days to tassel initiation from planting under long and short days were used to classify the cultivars according to their sensitivity. Francis et al. (1969) presented a system of classification based on sensitivity difference. According to them, cultivars with a sensitivity difference of more than 6 days were considered as sensitive, 4 to 6 days were considered intermediate and less than 4 days were photoperiod insensitive. In this preliminary screening, the method of Francis et al. (1969) was used with some modifications in the classification.

Difference in days to tassel initiation	Classification
<4	Insensitive
4-7	Intermediate or low sensitivity
8-11	Sensitive
>11	Highly sensitive

The intermediate grouping could be considered as a transitional group containing weakly insensitive and weakly sensitive cultivars.

3.2 Photoperiod Response Experiments in Corn

3.2.1 Response Under Different Photoperiods

Two photoperiod insensitive and two sensitive inbred lines were used in these growth chamber studies. The insensitive inbreds used were Oh43 and Va35, while the sensitive inbreds were Hi30 and Tx601. These 4 inbred lines were subjected to 4 different daylength conditions, 10, 12, 14, 16 hours. In the 10 hour daylight treatment, both the

fluorescent and incandescent lights were turned on except the last 15 minutes which was only incandescent. For the other daylength treatments, 12, 14, and 16 hours, the high intensity light was on for a period of 11 hours 45 minutes, and were supplemented with ¼ hour, 2¼ hours, and 4¼ hours incandescent light respectively. The light intensity of the incandescent light at the level of the pots was found to be about 1292 lux (120 ft-c). The 4 growth chambers were maintained at 60% relative humidity, 26.6°C day and 21.1°C night temperatures. Three of the chambers were of the same type as described in Section 3.1, however the fourth chamber used was of the walk-in type. This walk-in chamber had manual controls for the temperature settings while the smaller chambers had automatic temperature controls for day and night.

There were 40 pots (15 cm by 15 cm) per chamber and 10 pots were allocated to each inbred. Within each pot 15 seeds were sown on sterilized soil. Watering and fertilizer application was the same as described in Section 3.1. Seedlings were sampled on alternate days starting from the 6th day after sowing. For each inbred under each photoperiod condition, 4 seedling plants were sampled randomly on each sampling date. These plants were dissected for tassel length measurements. The number of fully emerged leaves was counted and the stage of tassel development classified as follows:

Stage 1: Meristem less than 0.4 mm from tip to the base of the youngest leaf initial. This stage was considered as vegetative.

Stage 2: Meristem 0.4 mm and above, but before the appearance of the spikelet primordia on the tassel. This was the stage of tassel initiation and was considered to be the beginning

of the reproductive stages.

Stage 3: Appearance of the spikelet primordia on the tassel.

Stage 4: Elongation of the basal branches of the tassel.

Stage 5: Appearance of spikelet primordia on the branches of the tassel.

Stage 6: Differentiation of spikelet initials on the central axis of the tassel.

Stage 7: Differentiation of spikelet initials on the tassel branches.

Stage 8: Differentiation of anther initials on the central axis of the tassel.

Stage 9: Differentiation of anther initials on the tassel branches.

Photomicrographs of some of these stages can be seen in Bonnett (1966). Dissections were terminated when the tassel had reached the 9th stage of development.

The experiment was repeated a second time and the four light treatments were reassigned randomly to the growth chambers. In this experiment, the start of the sampling for the different inbreds at the different photoperiod treatments were based on the results of the first set. Sampling began several days before tassel initiation. This was done to reduce the amount of laborious dissection as well as to conserve as many plants as possible for sampling at the later stages of tassel development.

These duplicate experiments were analyzed as a split-plot design with photoperiods (or chambers) as the main plots and the cultivars as subplots. The characters used for the statistical analysis were days to tassel initiation and number of fully emerged leaves at tassel initiation.

3.2.2 Short-day Effects on Photoinduction

Growth Chamber Studies:

Three cultivars consisting of a photoperiod insensitive inbred, Va35, a sensitive inbred, Tx601, and their hybrid Va35 x Tx601 was used for this study. Each of these cultivars were subjected to different numbers of short day treatments after seedling emergence. Seedling emergence was on the 4th day after sowing and was considered as day 0 for the short day treatments. The short day (SD) treatments used were 0 SD, 5 SD, 10 SD, 15 SD, 20 SD, 25 SD, 30 SD and CSD (continuous short day). After they were subjected to these treatments, they were transferred to another growth chamber and maintained under long days. The SD condition consisted of 10 hours of light with the last 15 minutes as incandescent only. The long day condition was 16 hours with 10 hour of full light (flourescent and incandescent) and the last 6 hours as incandescent. Four chambers of the type described in Section 3.1 were used, with two under short days, and two under long days.

Two pots (15 cm by 15 cm) were used for each cultivar per treatment. In each pot, 14 seeds were sown on sterilized soil. Watering, fertilizer application, temperature and humidity were the same as in previous experiments. Four plants per treatment were sampled for dissection every ten days beginning 20 days from planting. However, excess pots were added for the 0 SD (i.e. long day) and CSD treatments, so that on each transfer date, plants were sampled to check if tassel initiation had occurred.

A split-plot design with two replications was used in this study with genotypes as main plot and light treatments as subplot.

Mean tassel lengths from the different sampling days were used to estimate the days to tassel initiation (DTI). This could be obtained by plotting tassel length on the log scale against time on a semi-logarithm graph paper (Section 4.2). Tassel initiation was again considered to have occurred when the meristem reached a length of 0.4 mm. Values of DTI were used for the statistical analysis.

Greenhouse Studies:

A photoperiod sensitive hybrid, CM104 x Tx601, was planted on June 1, 1977 in the greenhouse facilities at Magoon, University of Hawaii Upper Campus. These were exposed to different short day cycles, and for these treatments, plants were placed in a section of a greenhouse in which they were exposed to normal daylength. Percentage light within the greenhouse was estimated to be around 32%. The average daylength was about 13 hours at the period this experiment was conducted, and this constituted the short-days.

For each photoinductive treatment, 3 pots constituted a plot. In each pot (22.2 cm diameter by 21.6 cm deep) 4 seeds were sown, and later thinned to 2 plants per pot. The pots were watered daily at the beginning, and twice a day at the later stage. A tablespoon of NPK 15-15-15 was applied to each pot once a week. The photoinductive cycles used, starting from the day of planting, were 0 SD, 10 SD, 20 SD, 30 SD, 40 SD, 50 SD and CSD (continuous short day). After these treatments, they were moved to another section of the greenhouse in which incandescent lamps were set up, operated by a timer to extend the daylength by 4 hours, which constituted the long-days.

Three benches were used, each constituting a replicate. On each bench, 3 incandescent light bulbs (Westinghouse Standard Bulbs --

60 watts) were strung (using wooden frames as support) 180 cm above the bench, with the bulbs spaced at a distance of 120 cm (Figure 1). The light intensity at the level of the pots was found to be around 86 lux (8 ft-c).

This experiment was set up as a randomized complete block design with 3 replicates. Data were collected on days to anthesis (first pollen shed).

3.2.3 Long-day Effects on Photoinduction

Growth Chamber Studies:

Photoperiod insensitive inbred Va35 and sensitive inbred Tx601 and their hybrid were kept under long days of 16 hours with at least 6 hours as incandescent light. The long day periods were 0 LD, 10 LD, 20 LD, 30 LD, 40 LD, 50 LD and CLD (continuous long day) after sowing. They were then transferred to short day chambers (10 hours with last 15 minutes as incandescent light) for photoinduction. Four chambers were used with 2 chambers under short days and 2 under long days, thereby constituting 2 replicates for this experiment. Watering, fertilizer application, temperature and humidity settings were the same as described in Section 3.2.2.

Starting on the 21st day from planting, 4 plants from each treatment were dissected to measure the length of the tassel. Sampling was done on a regular 10 day interval. These data were used to estimate the number of days to tassel initiation (as described in Section 3.2.2). Mean values of DTI were used for the statistical analysis using a split plot design with the genotypes as main plot and light treatments as subplot.

Figure 1. Light set-up for photoinduction studies in the greenhouse

Greenhouse Studies:

In this experiment, the set up was similar to the one described in Section 3.2.2, as they were planted on the same day, but with different treatments. The materials used was CM104 x Tx601, a photoperiod sensitive hybrid. In this case, they were kept under long days in a section of the greenhouse by supplementing natural day light with 4 hours of incandescent light. The treatments used were 0 LD, 10 LD, 20 LD, 30 LD, 40 LD, 50 LD, 60 LD, 70 LD, 80 LD, 90 LD and CLD. After this, they were moved to another house where they were grown under normal daylength (average 13 hours) for photoinduction. A randomized complete block design with 3 replicates was used in this experiment. Data was collected on days to anthesis.

3.3 Genetic Studies

3.3.1 Field Experimental Procedures

All field experiments were conducted at the University of Hawaii Research Station at Waimanalo. The Research Station is located at 21°N in Oahu, Hawaii, and it has a Typic Haplustoll subgroup soil type. The soil is silty clay with a pH of 6.5. Standard field preparations include a herbicide application of Sutan, and a preplant fertilizer application equivalent to 150-120-90. Corn plants were usually sidedressed with 67.2 kg/ha of N after thinning. Unless otherwise stated, all field trials carried out in this study were sown with 3 seeds per hill, and thinned down to one plant per hill after 4 weeks to give a population of about 60,000 plants per hectare (24,000 plants per acre). Planting distances used were 76.2 cm between rows (30 inches) and 22.1 cm between plants (8.7 inches). A thick border was planted around the edge

of the experimental materials. Overhead sprinkler irrigation was standard and on a 5-day schedule.

Light Set-Up:

A supplementary lighting system was set up in the field at Waimanalo Research Station to facilitate studies on the genetics of photoperiod sensitivity in corn. This system was set up with consultative help from the Hawaiian Electric Company. A general overview of this set-up is shown in Figure 2.

Eight electric poles were erected four on each side of the field, spaced about 51.2 m apart. The distance between poles on the same end was 4.6 m. Guide wires or cables were strung between opposite poles at a height of about 3.4 m above the ground. Two No. 12 standard wires (single copper conductor) were also strung and were tapped onto the guide wires at different points. The head and tail ends were looped round a porcelain wire holder fixed on each pole. The head ends were connected to a main cable (No. 4 Triplex Aluminium Wire), which was supported on one end by a electric pole and the other by the Station Office roof, with the use of a preformed deadend.

Forty 150 watt incandescent flood lamps (Westinghouse-150 PAR/FL) were used to light up the field at night. On each line there were 10 lamps, which were screwed into a plastic "pink" socket. These sockets had hooks which were hung onto the guide wires for support. Lamps were spaced 4.6 m from one another on a line. Lamps on adjacent lines were staggered to provide more uniform light distribution.

The main cable was connected to a 240 volt power source, but the secondary wires in the field were connected to the main cable in a "split voltage" system to provide 120 volts for the lamps. The

Figure 2. Light set-up for photoperiod studies in the field at the Waimanalo Research Station

whole system was controlled by two 30 amp circuit breakers (single pole) which were turned on when in use. A clock timer was hooked up to activate or deactivate a 3-pole magnetic contactor (220 volts, 40 amps), which would supply the power source to turn the lamps on or off. In order to prevent sagging of the wires, two bamboo supports on each line kept the lamps at almost constant height. In addition, support cables or "deadmen" were erected on each electric pole. This set-up provided an average light intensity of about 161.5 lux (15 ft-c), with about 21.5 - 32.3 lux (2 - 3 ft-c) at the weakest spots, measured at ground level.

3.3.2 Genetics of Photoperiod Sensitivity: Diallel Analysis

A 10 entry diallel cross involving photoperiod insensitive, intermediate and sensitive inbreds was set up to study the genetics of photoperiod sensitivity in corn. The inbreds used were Va35, Oh43, B37, A619, Mo17, Hi25, Hi26, Hi30, CM104 and Tx601, which ranged from highly photoperiod insensitive to highly photoperiod sensitive inbreds (Table 2 of section 4.1). The 45 single crosses without reciprocals, and the parental lines were planted on March 15, 1977 under normal as well as extended daylength. A 20-hill plot was planted in both light regimes. The average daylength for the duration of this experiment was about 12.5 hours from sunrise to sunset. However, with the inclusion of civil twilight with a minimum of 5 ft-c (Francis, 1972b), the average daylength was 13.3 hours. An additional 4 hours of light was added to extend the daylength for the materials grown under supplementary light. Lights were turned on from seedling emergence to 90 days after planting.

This experiment was set up in a strip block design with 3 replications. The characters studied were as follows:

1. Days to anthesis: The time from planting to the day of first pollen shed.

2. Days to silking: The time from planting to the day of silk emergence.

3. Plant height (cm): The height from the ground to the tip of the central axis of the tassel.

4. Ear height (cm): The height from the ground to the base of the topmost ear.

5. Cob length (cm): This has often been referred to as ear length, and is measured from the tip of the cob to the butt.

6. Filled ear length (cm): Ear length containing fully developed kernels.

7. Row number: Number of kernel rows at mid-ear.

8. Kernels per row: The average number of fully developed kernels of 3 random rows from each ear.

9. Kernel depth (cm): Ten randomly selected kernels were measured using a vernier caliper and averaged.

10. Ear weight (gm): The dried ears of 10 plants were weighed and averaged.

11. Grain yield (gm): After shelling grains were weighed and grain yield expressed in metric tons per hectare assuming perfect stand.

12. 100 kernel weight (gm): 100 randomly selected kernels were weighed, and the mean value computed.

Data were collected from the middle 10 plants of each plot, and the mean values were used for analysis of variance. Plants which were infected and stunted by maize mosaic virus were not included.

All weight measurements were adjusted to 15.5% moisture.

In addition, the differential response (i.e. difference of the values under the two photoperiods) of days to anthesis and days to silking under the normal and extended daylength were used for the diallel analysis following Method 2- Model 1 of Griffing's combining ability analysis (1956) using plot means.

In order to obtain more information for the genetic studies, a 5x5 diallel was extracted from the above 10 entry diallel. The entries consisted of highly photoperiod sensitive inbreds, CM104 and Tx601, as well as inbreds Va35, B37 and Oh43 which were photoperiod insensitive. For these entries, the plot size planted was a 30-hill plot and they were grouped together during randomization for convenience in planting as well as subsequent sampling. Additional characters studied for this 5 entry diallel were:

1. Days to tassel initiation (DTI): Four plants from each plot were randomly selected for dissection at different intervals. Tassel length was measured and the mean values were used to estimate DTI.

2. Days for tassel development (DTD): The period from tassel initiation to pollen shed, estimated by subtracting DTI from days to anthesis.

3. Kernel initials per row: Kernel initials from 4 ear shoots per plot at silking were averaged.

4. Leaf number: The number of leaves from 10 plants within each plot were counted including those initial leaves which had dropped off, and the mean leaf number computed.

The differential responses (i.e. long day value minus short day value) of these four characters based on plot means were used for the graphical analysis of Hayman and Jinks (Hayman, 1954b) as well as combining ability analysis of Griffing (Method 2- Model 1). A correlation matrix was set up involving the characters, DTI, DTD, leaf number, days to anthesis and days to silking.

The same set of the 10 entry diallel cross was planted at the South Farm, University of Illinois on May 24, 1976 which had long summer days at that time. This was planted as a randomized complete block design with 2 replications. Days to anthesis and days to silking were collected. In this case, the differential response was obtained by subtracting the mean of the 3 replicates planted under normal light (at the University of Hawaii Waimanalo Research Station) from the two replicates planted in Illinois. This was subjected to the combining ability analysis based on plot mean data.

3.3.3 Genetics of Photoperiod Sensitivity: Generation Mean Analysis

The parental (P1 and P2), F1, F2, and backcross (B1 and B2) populations derived from crosses between photoperiod insensitive and photoperiod sensitive inbreds were evaluated under long days to study the genetics of photoperiod sensitivity. P1 and P2 were applied to the photoperiod insensitive and sensitive inbreds, respectively; B1 was the backcross of the F1 to P1, etc. Different long day environments were used in this study involving different sets of crosses:

University of Hawaii -- The following sets were planted on March 15, 1977 under extended daylength. They were: B37 x CM104, B73 x CM104, Oh43 x CM104, Va35 x CM104 and B37 x Tx601.

University of Illinois -- These were planted on May 24, 1976 under natural long days. These were Oh43 x Hi30, Va35 x Hi30, Oh43 x Tx601 and Va35 x Tx601.

University of Nebraska -- These were planted on May 17, 1977 under natural long days. The sets were B73 x Hi30, Va35 x Tx601 and B73 x Tx601.

The populations planted at the University of Hawaii consisted of 1 row each of P1, P2 and F1, 2 rows each of B1 and B2, and 8 rows of F2. Each row had 10 hills with 2 plants per hill.

The populations planted at the University of Illinois and the University of Nebraska had the same number of rows as the University of Hawaii planting except for the F2 population which had only 6 rows. The number of hills planted at the University of Illinois and the University of Nebraska were 9 and 10 respectively. However, in some cases, there were 14 hills at the University of Nebraska planting. All had two plants per hill. The population size at the University of Illinois was much lower than what was planted because of poor germination.

Genetic effects of a six parameter model were estimated from generation mean analysis (Hayman, 1958, 1960) using Gamble's notations if they failed to fit a three parameter model (Mather and Jinks, 1971). Estimates of additive, dominance and environmental variances (Mather and Jinks, 1971) were calculated based on the assumption that there was no epistasis and no linkage involved. The following formulas were used to derive these variances:

$$V_A = 2VF_2 - (VB_1 + VB_2)$$

$$V_D = VF_2 - (V_A + V_E)$$

$$V_E = \frac{VP_1 + VP_2 + VF_1}{3}$$

Estimates of the six population variances were obtained by pooling the within row sum of squares over replicates in the analysis of variance.

Narrow sense heritability was calculated following Warner's (1952) formula:

$$nh^2 = \frac{2VF_2 - (VB_1 + VB_2)}{VF_2}$$

Broad sense heritability was also calculated in the conventional way, i.e.

$$bh^2 = \frac{V_A + V_D}{V_A + V_D + V_E}$$

The minimum number of genetic factors affecting photoperiod sensitivity was estimated by

1) the Castle-Wright formula (Mock and Schuetz, 1974) which was given by:

$$n = (P1 - P2)^2/8(V_{F2} - V_{F1})$$

2) a formula attributed to Sewall Wright (Mock and Schuetz, 1974)

$$n = (0.25(0.75 - h + h^2)D^2/(V_{F2} - V_{F1})$$

where

$$D = P_2 - P_1 \text{ and } h = (F_1 - P_1)/D$$

3.3.4 Diallel Analysis of Seasonal Plantings

The same set of 10 entry diallel crosses described in Section 3.3.2 was also planted under winter conditions at the University of Hawaii Research Station at Waimanalo. This was planted on November 4, 1976. The other planting was the one under normal daylength (Section 3.3.2) planted on March 15, 1977. This planting was actually a spring-summer planting, but was considered as a summer crop here since the weather conditions during a greater part of spring in 1977 were somewhat like summer.

Each planting was set up in a randomized block design with 3 replicates. Combining ability analyses (Griffing, 1956) of the two seasons were carried out for grain yield, and some yield components, i.e. cob length, kernels per row, and 100 kernel weight. These analyses were based on plot mean data.

3.4 Date of Planting Experiments

Six hybrids were chosen for a monthly planting beginning on October 14, 1975 for a period of 20 months. The six hybrids used were:

H652 - (CM105 x Oh545)
H763 - (Ant2 x B68)
H787 - (B68 x B37)
H814 - (A632 x A619)
H815 - (CM111 x CM104)
H816 - (Tx601 x CM111)

These hybrids are derived from tropical x temperate crosses (H652 and H763), temperate x temperate crosses (H787 and H814) and tropical x tropical crosses (H815 and H816). Plantings were made on the second

Tuesday of every month. Occasional plantings were delayed a day or two by rain.

Each experimental plot had 25 hills planted with 2 seeds per hill which were thinned to one plant after 4 weeks. The usual planting distance was 76.2 cm between rows and 22.1 cm within the row. A drip irrigation system was installed to irrigate the plots at least twice a week. Borders using a corn hybrid were planted around each planting.

The experimental design used was a randomized complete block design with 2 replications. Data were collected for the following characters: days to mid-silk, plant height, ear height, cob length, filled ear length, row number, kernels per row, kernel depth, ear weight, grain yield and 100 kernel weight. Days to mid-silk was collected when 50% of the plants within each plot had silked. Measurements for the other characters had been previously described. Data were all expressed on plot mean basis. All weight measurements were adjusted to 15.5% moisture.

Combined analyses of variance were carried out for all characters. In addition, multiple regression analysis was carried out with grain yield as a dependent variable and the 3 monthly means of solar radiation, mean maximum and minimum temperatures, and mean daylength during the period of development as the independent variables.

4. PHOTOPERIOD RESPONSE IN CORN

4.1 Screening for Insensitivity to Photoperiod

Forty three inbreds and two hybrids were tested for photoperiod sensitivity under long-day (16 hour) as well as short-day (12 hour) conditions in separate growth chambers. Plants were sampled and dissected on alternate days to determine tassel initiation time. A sensitivity difference for each genotype was obtained by subtracting the short day value from the long day value (Table 2).

Genotypes which differentiated tassels with differences of less than 4 days under long and short days were considered insensitive to changes in photoperiod. Those with a difference of 4 to 7 days were considered as intermediate genotypes or low sensitivity. Sensitivity difference of 8 to 11 days were sensitive while those with a difference of more than 11 days were regarded as highly sensitive. DTI values for some genotypes under long days were not well defined, since there were too few plants for adequate sampling. Nevertheless, these could still be classified except F44, 74-1653-2, 74-1711-1, 74-1721-3, 74-1744-2 and 74-1756-1. Sensitivity percentage was also computed (Table 2). This was taken as the difference between the two daylength values, divided by the short-day value and expressed in percentage. This could also form the basis of classification for photoperiod sensitivity.

Earliness was not associated with insensitivity, since genotypes which initiated their tassel early occurred among photoperiod insensitive and sensitive inbreds. Genotypes from the tropics and subtropics tend to be photoperiod sensitive (Section 3 - Table 1). Genotypes from the temperate regions, on the other hand, contained a wide degree of

Table 2. Days to tassel initiation of genotypes under 12- and 16-hour daylength

Genotypes	16-hr	12-hr	Sensitivity difference	Sensitivity percentage
A619	36	32	4	12.5
AA8	34	26	8	30.8
B37	27	24	3	12.5
B68	36	29	7	24.1
B73	27	24	3	12.5
CI64	>44	29	>15	>51.7
CI66	44	27	17	63.0
CM103	45	34	11	32.4
CM104	46	36	10	27.8
CM105	>42	32	>10	>31.2
CM109	>44	34	>10	>29.4
CM111	>38	30	> 8	>26.7
CM201	43	32	11	34.4
F44	>38	36	> 2	> 5.5
Ga209	>40	30	>10	>33.3
H95	>46	31	>15	>48.4
Hi25 (B14A)	30	23	7	30.4
Hi26 (CI21E)	43	33	10	30.3
Hi30	36	24	12	50.0
Mo17	30	25	5	20.0
Mp68:616	44	34	10	29.4
N6G	35	24	11	45.8
N28	35	26	9	34.6
Oh43	24	22	2	9.1
Oh545	33	27	6	22.2
Tx601	>50	32	>18	>56.2
Va35	29	29	0	0.0
W64A	42	31	11	35.5
442	36	20	16	80.0
74-1610	44	36	8	22.2
74-1625-1	42	26	16	61.5
74-1629-3	>38	30	> 8	>26.7
74-1645-4	>46	30	>16	>53.3
74-1653-2	>38	32	> 6	>18.8
74-1665-1	36	32	4	12.5
74-1675-2	48	36	12	33.3
74-1711-1	>38	36	> 2	> 5.6
74-1721-3	>38	34	> 4	> 2.9
74-1744-2	>38	36	> 2	> 5.6
74-1756-1	>36	35	> 1	> 2.8
74-1788	38	24	14	58.3
74-1810-2	>38	30	> 8	>26.7
74-1819-2	>46	35	>11	>31.4
Hybrids:				
H68b	42	26	16	61.5
X306B	>46	32	>14	>43.8

Genotypes with sensitivity difference of less than 4 days were insensitive, 4 - 7 were low sensitivity or intermediate, 8 - 11 days were sensitive and more than 11 were highly sensitive

sensitivity types, dominated by genotypes which were much less sensitive to photoperiod changes. However, the following temperate genotypes H95, N6G, N28, and W64A were sensitive to photoperiod changes. This might appear questionable but it might also be possible that these genotypes were very early maturing types under tropical conditions than temperate by virtue of its photoperiod sensitivity. In view of the fact that this screening was not repeated, no concrete conclusions could be drawn at this time regarding the nature of its photoperiod sensitivity. Hi26 would be classified as sensitive according to the results in Table 2. In subsequent studies, it was found that it was not as sensitive but intermediate in sensitivity.

4.2 Tassel Development Under Different Photoperiods

Photoperiod response of 4 inbreds was studied under daylengths of 10, 12, 14 and 16 hours in growth chambers. Inbreds Oh43 and Va35 were classified as photoperiod insensitive, while Hi30 and Tx601 were photoperiod sensitive (Table 2). Dissecting plants to measure tassel length revealed the following pattern of development. At the time of germination, meristem length was less than 0.2 mm. Between 2 and 6 days from the time of seedling emergence, meristems reached a length of 0.2 mm and remained at this length during most of the vegetative phase. Under long day conditions the meristem of photoperiod sensitive materials (Hi30 and Tx601) remained at 0.2 mm for a longer period than the photoperiod insensitive inbreds (Va35 and Oh43). A transitional period of 1 or 2 weeks occurred when the growing point was about to change from the vegetative to the reproductive phase. During this transition, the meristem was elongating slowly. A length of 0.4 mm was taken to be the stage of

tassel initiation (Siemer et al., 1969). Differentiation of the tassel was very rapid after tassel initiation and elongated on a logarithmic scale until nearly full development.

Growth of the tassel was clearly exponential, and plotting on semi-log graph paper produced a straight line from tassel initiation onwards. Regression equations of the form $\log Y = a + bX$ were computed from about 0.4 mm for the 4 inbreds under the four daylength treatments (Table 3). Highly significant correlation coefficients were obtained for these relationships in most cases. The effects of daylength on tassel length during the tassel development phase plotted on semi-log graph paper are shown in Figures 3-6. These graphs indicate the nature of photoperiod sensitivity, the rate of development and also the critical daylength for photoperiodic reactions.

The regression showed little or no difference in response between 10 and 12 hour daylength for all the inbreds studied. As daylength was increased, time of tassel initiation was delayed and the regression lines were spread further apart depending on the nature of photoperiod sensitivity. The photoperiod insensitive inbred Va35 (Figure 3) had all the four regression lines quite close to one another as compared with all the other inbreds. Oh43, another insensitive inbred, was found to be weakly insensitive from these regression lines (Figure 4).

The 12 hour daylength regression line and that of the 14 hour daylength were furthest apart in Hi30 (Figure 5). On the other hand, this occurred between the 14 hour and 16 hour daylength in Tx601 (Figure 6). These delays in days to tassel initiation are also presented in Table 4. The difference between the 14 and 16 hour treatment for days to tassel

Table 3. Regression equations and correlation coefficient of tassel length (mm) on days from planting in four inbreds under four different photoperiods

HA30	Regression equation	r
10 hr	log Y = -2.455 + 0.078X	0.98**
12 hr	log Y = -2.772 + 0.085X	0.99**
14 hr	log Y = -4.770 + 0.104X	0.84*
16 hr	log Y = -4.357 + 0.081X	0.92**
Homogeneity of regression coefficients, F = 6.431**		
Oh43		
10 hr	log Y = -2.452 + 0.093X	0.99**
12 hr	log Y = -1.852 + 0.074X	0.97**
14 hr	log Y = -2.108 + 0.065X	0.93**
16 hr	log Y = -2.344 + 0.061X	0.95**
Homogeneity of regression coefficients, F = 4.15*		
Tx601		
10 hr	log Y = -2.999 + 0.071X	0.97**
12 hr	log Y = -3.443 + 0.082X	0.97**
14 hr	log Y = -6.403 + 0.130X	0.96*
16 hr	log Y = -5.506 + 0.090X	0.90*
Homogeneity of regression coefficients, F = 0.655 NS		
Va35		
10 hr	log Y = -2.056 + 0.076X	0.98**
12 hr	log Y = -2.380 + 0.086X	0.99**
14 hr	log Y = -2.722 + 0.088X	0.98**
16 hr	log Y = -2.710 + 0.078X	0.98**
Homogeneity of regression coefficients, F = 0.574 NS		

*, ** Significant at 5% and 1%, respectively

NS - Non-significant

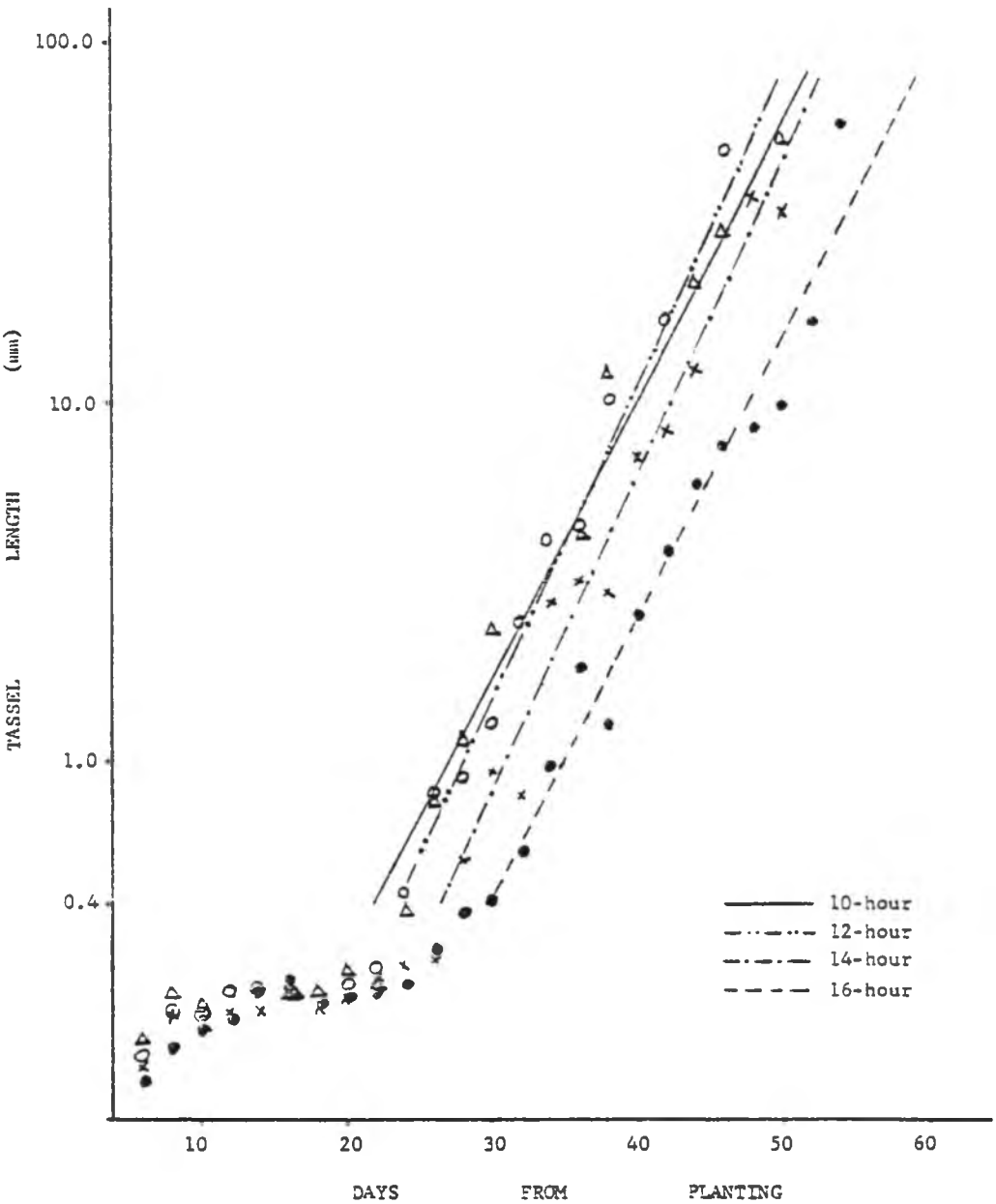

Figure 3. Growth of tassel in mm. for Va35 at different photoperiods

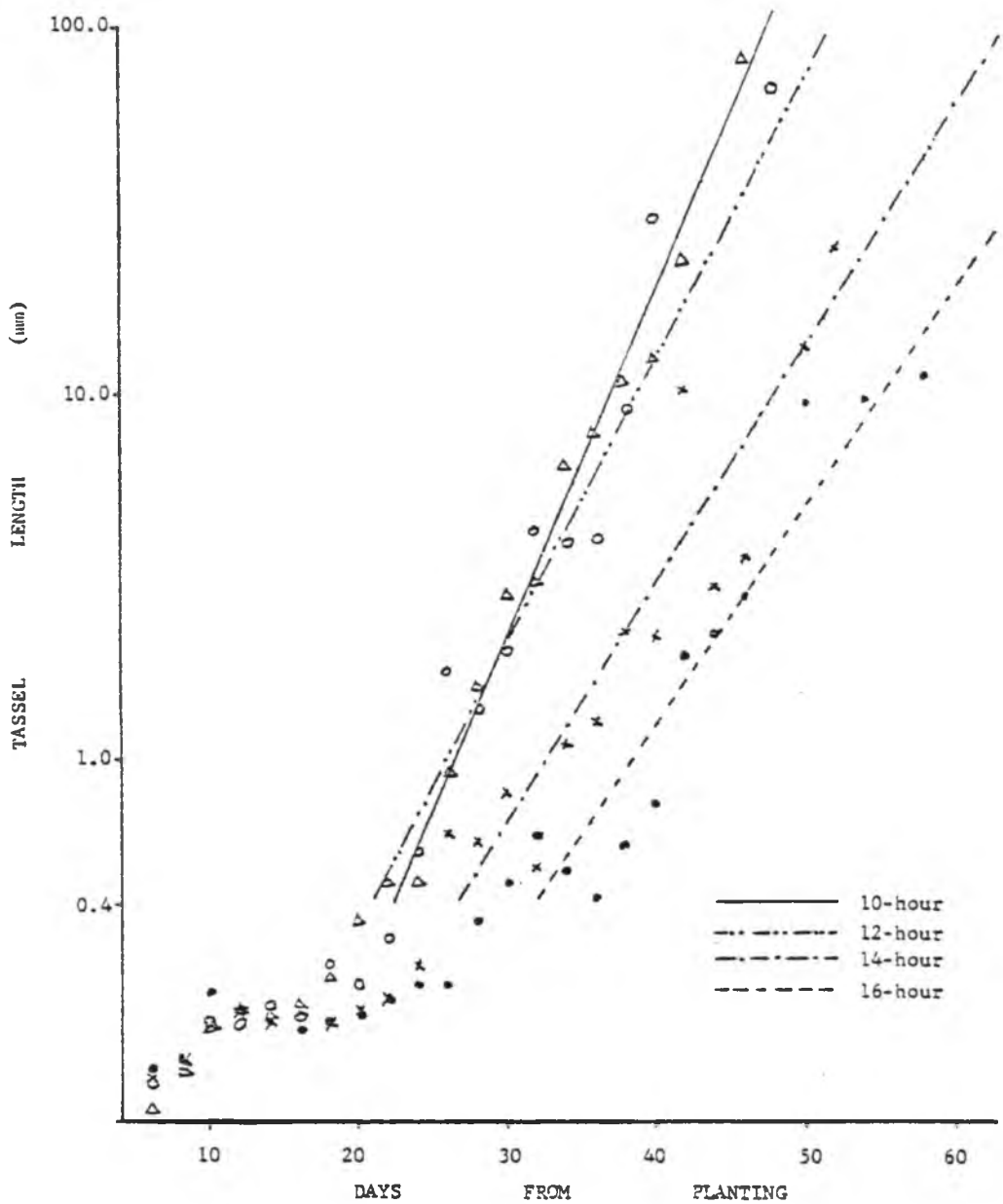

Figure 4. Growth of tassel in mm. for Oh43 at different photoperiods

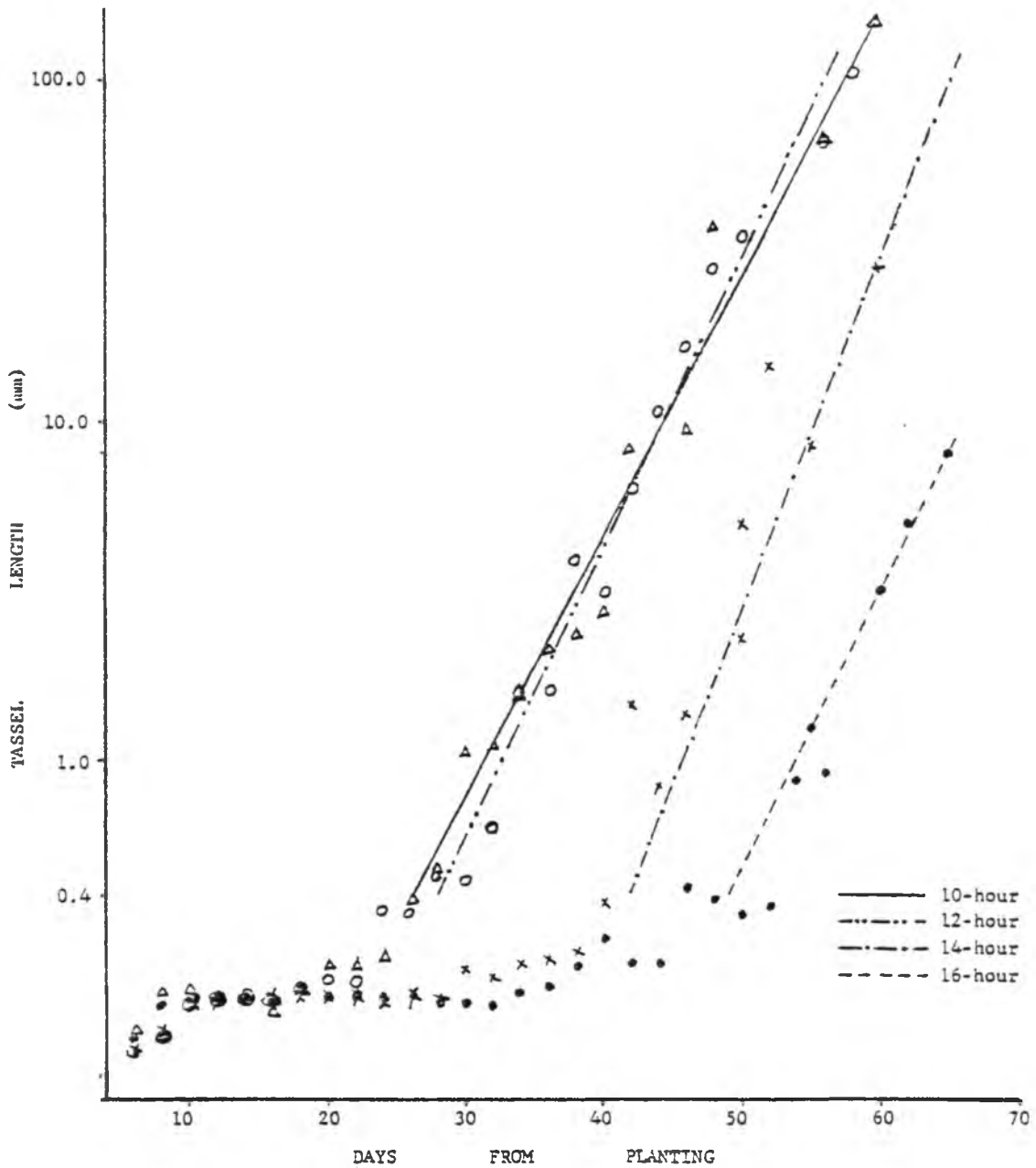

Figure 5. Growth of tassel in mm. for Hi30 at different photoperiods

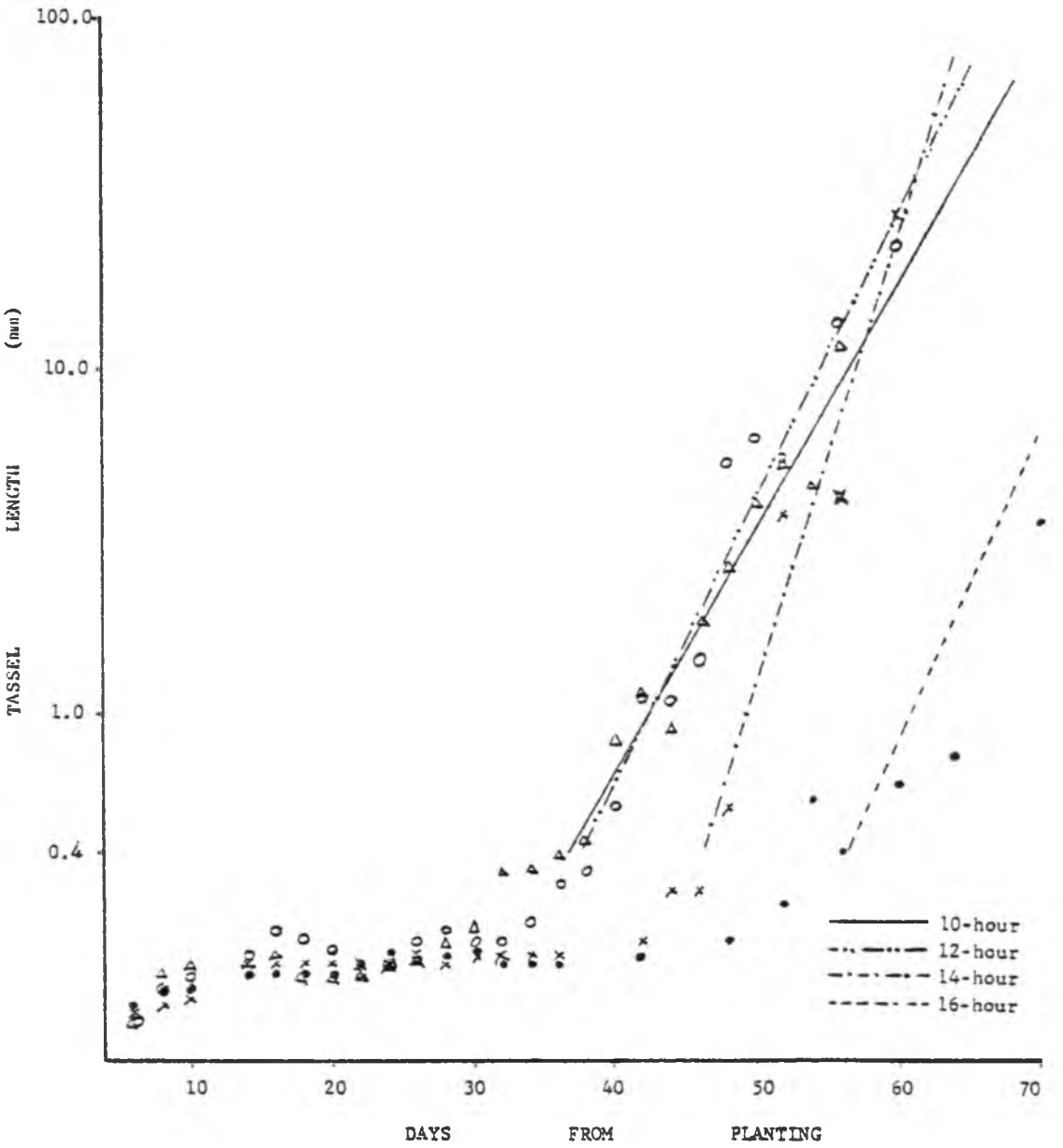

Figure 6. Growth of tassel in mm. for Tx601 at different photoperiods

initiation in Hi30, although not statistically significant, was also quite great. In Tx601, the difference between the 12 and 14 hour was a delay of 13 days, while it was 18 days between the 14 and 16 hour treatment. This was statistically different.

The slopes of the regression lines under different daylength regimes of each inbred did not appear to be parallel. However, in testing the differences between the slopes of each inbred using the homogeneity of regression coefficients as outlined by Steel and Torrie (1960), it was found that no significant differences occurred among slopes of Tx601 and Va35 (Table 3). The slope of the 14 hour daylength regression line in Tx601 appeared to be greatly different from the rest, although no significant difference was detected. This could possibly be due to the smaller number of paired observations as compared with the number used in computing the other regression lines. On the other hand, significant differences at 5% and 1% were found among the slopes of the different photoperiods in Oh43 and Hi30, indicating differences in the rate of tassel development under different daylengths.

Stages of tassel development classified on a scale of 1 to 9 were also plotted against days from planting (Figure 7). Stage 1 was vegetative, while stage 2 was the stage of tassel initiation. The other stages were used to indicate the different stages of the reproductive phase. Unlike tassel length, these assumed a straight line relationship with time. Results regarding the photoperiod sensitivity, rates of development and critical daylength could also be derived from these graphs.

Data on days to tassel initiation (DTI) as well as emerged leaf number at tassel initiation for the four inbreds under the different

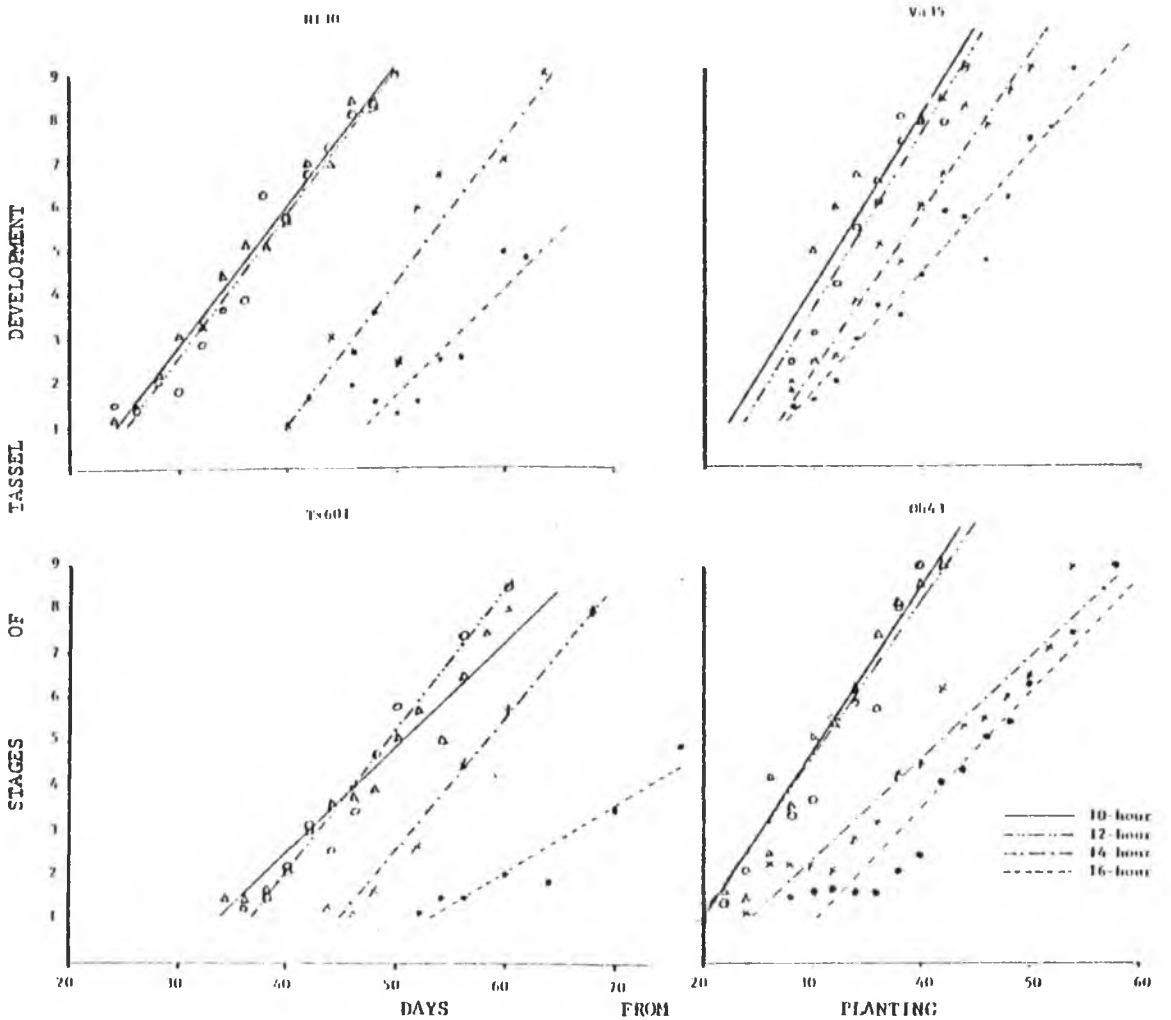

Figure 7. Growth stages of tassel development for different inbreds at different photoperiods

daylengths were also collected (Table 4). Analysis of variance (Table 5) of DTI detected no significant difference among the daylength treatments. However, significant differences were found between the inbreds as well as the daylength x inbreds interaction. Significant differences were found in all these three sources of variation when emerged leaf number at TI was analyzed.

The means of DTI and leaf number are shown in Table 4. The Bayes least significant difference (BLSD) indicated no significant difference among daylength treatments on Oh43 and Va35 in the two characters studied, thereby suggesting their photoperiod insensitive nature. In the case of Hi30 and Tx601, the daylengths of either 14 or 16 hours brought about a significant delay in DTI. Similarly, under longer daylengths, tassel initiation in these two sensitive inbreds occurred at a higher leaf number under long days than under short day treatments. These differences can best be illustrated with the response curves in Figures 8 and 9. These graphs also showed that the shorter the daylength the earlier was the tassel initiation especially in Hi30 and Tx601. In this case, the optimum daylength for tassel initiation was the 10 hour day.

4.3 Short-day Effects on Photoinduction

Growth Chamber Experiments:

The exposure of three genotypes of differing sensitivity to different numbers of short day treatments brought about the differences in response trends. The results are presented in Table 6. Missing data (due to shortage of plants) occurred in the 5 SD, 10 SD and 20 SD treatments of Tx601, and these treatments for all genotypes were excluded in the analysis of variance. The sources of variation for genotypes, SD treatments and SD x genotype interaction were highly significant (Table 7).

Table 4. Average days to tassel initiation (DTI) and emerged leaf number at tassel initiation (TI) of four inbreds under four different daylengths

Day-length	DTI (days)				Emerged leaf no. at TI			
	HA30	Oh43	Tx601	Va35	HA30	Oh43	Tx601	Va35
10 hr	27	23	35	27	3.6	3.2	5.2	3.9
12 hr	29	24	38	26	3.6	2.9	5.6	3.6
14 hr	44	26	51	28	4.6	3.3	6.8	3.9
16 hr	53	31	69	29	6.2	3.6	9.6	4.0
Interaction BLSD (0.05) = 13.2					1.02			

Table 5. Analysis of variance of data in Table 4

Source	d.f.	Mean Square	
		DTI	Emerged leaf no. at TI
Rep	1	60.50	0.01
Daylength	3	526.33	6.43*
Error (a)	3	107.50	0.24
Inbreds	3	862.33**	19.53**
Daylength x Inbreds	9	96.67*	1.61**
Error (b)	12	23.75	0.30

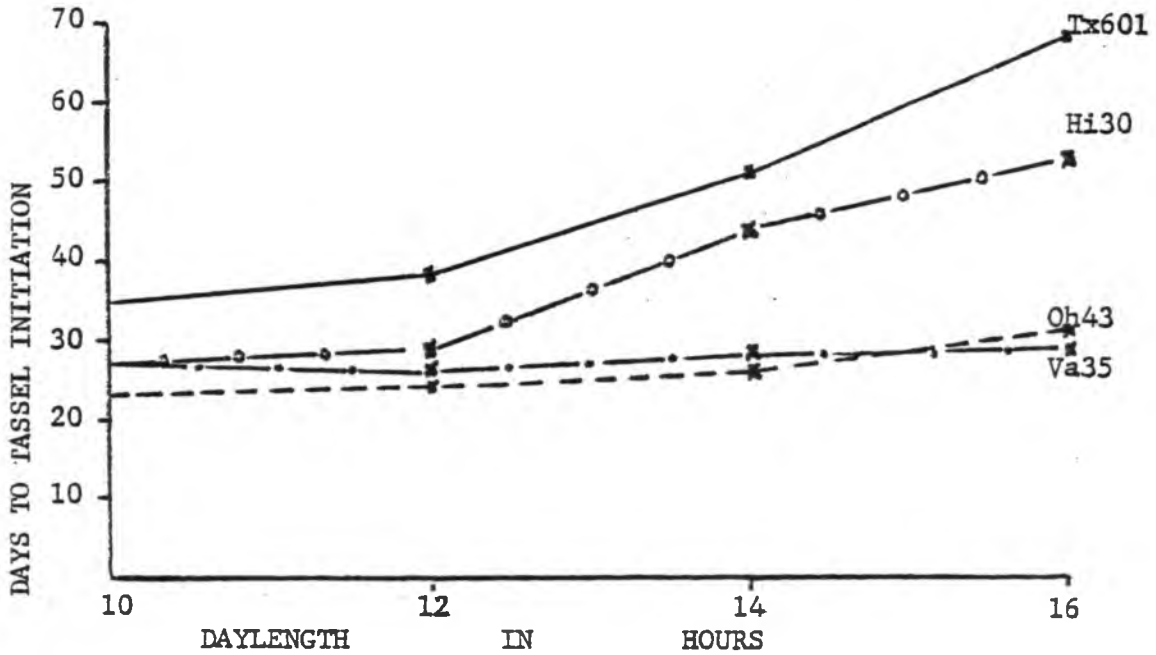

Figure 8. Days to tassel initiation under different photoperiods for four corn inbreds.

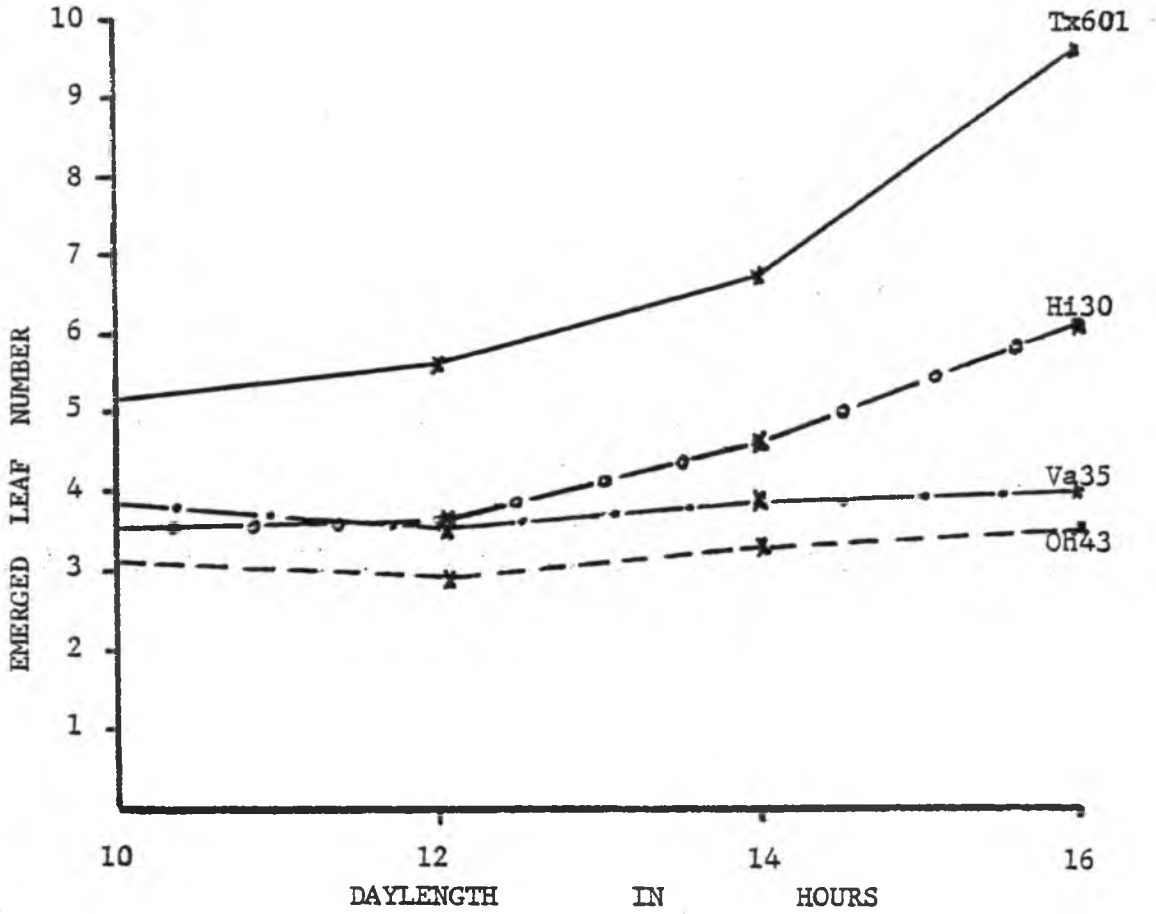

Figure 9. Emerged leaf number at tassel initiation under different photoperiods for four corn inbreds.

Table 6. Average days to tassel initiation of three genotypes exposed to different number of SD (followed by LD)

SD cycles	Va35	Tx601	Va35 x Tx601
0 SD	34.0	67.0	47.5
5 SD	42.5	--	50.0
10 SD	42.5	--	54.5
15 SD	42.0	69.0	61.0
20 SD	49.5	--	48.0
25 SD	33.0	57.0	34.0
30 SD	34.5	40.5	33.0
CSD	30.5	37.5	29.5

Interaction BLSD (0.05) = 4.3

Table 7. Analysis of variance of data in Table 6

Source	d.f.	Mean Square
Rep	1	0.14
Genotype	2	981.74**
Error (a)	2	2.53
SD	4	2455.00**
SD x Genotype	8	783.20**
Error (b)	12	79.80

(Treatments with missing value were excluded in the analysis)

It must be pointed out that SD treatments were considered here as after seedling emergence, which was 4 days from planting. Thus, a 5 SD treatment would indicate a total of 9 days under SD from planting.

In the photoperiod insensitive genotype, Va35, no significant differences in DTI were observed among 0 SD (i.e. CLD or continuous long day), 25 SD, 30 SD and continuous SD (CSD). However, sensitivity to photoperiod seemed to occur when the plants were usbjected to 5 SD, 10 SD, 15 SD and 20 SD treatments followed by long days.

In Va35, the number of short day treatments followed by long days should not have any significant effect on days to tassel initiation. However, inconsistent results were obtained for some treatments on increasing the number of short days. This may possibly be the result of small sample size used in dissections as well as the occasional breakdowns in the growth chambers used. It also appeared as though long days were negating the effects of short days in Va35 for the treatments 5 SD, 10 SD, 15 SD and 20 SD, and that the negating effects disappeared with a greater number of short days. However, data were inconclusive as there was no significant difference between the CSD and CLD. Furthermore, the reverse experiment (i.e. exposing plants to SD after different number of LD) did not show any big differences in DTI values (Table 8).

Similarly, the results of short day treatments followed by long days in Va35 x Tx601 also showed inconsistency in the DTI values (Table 6). There were some missing values in Tx601 and this was due to insufficient plants for extimating time of tassel initiation.

Greenhouse Experiments:

In a similar experiment conducted in the greenhouse with a photoperiod sensitive hybrid, CM104 x Tx601, plants were subjected to 0 SD, 10 SD,

20 SD, 30 SD, 40 SD, 50 SD, and continuous SD treatments followed by long days. A randomized complete block design was used with three replicates. Exposing plants to 10 and 20 photoinductive short days from planting did not bring about significant differences in days to anthesis as compared to the 0 SD (or CLD) treatment (Appendix 1). This would mean that CM104 x Tx601 was not responsive to daylength during the first 20 days from planting. Beyond these 20 days, days to anthesis were decreased with higher number of short-day treatments. Additional short days beyond thirty did not cause any great differences in days to anthesis (Figure 10). From field experiments (Section 5) it was known that tassel initiation in CM104 x Tx601 occurred, on the average, 29 days from planting under natural daylength conditions in Hawaii. Assuming that this was the same as under the greenhouse experiments, then the phase responsive to photoperiod occurred between 20 and 30 days after planting and the inductive phase must be quite short with an upper limit of 9 days. The 30 SD treatment therefore would have initiated its tassel at the time of transfer to long days. However, the days to anthesis for 30 SD were still significantly greater than the continuous short day treatment. This would suggest that tassel development (i.e. time from TI to anthesis) was also affected by photoperiod, but there was a photoperiod responsive and a non-responsive phase. This reproductive responsive phase appeared to be of a maximum of 11 days in duration (between TI and 40 SD treatments), after which additional short days would not make any difference in days to anthesis (as shown by the data of 40 SD, 50 SD and CSD treatments). Thus, a threshold number of inductive cycles starting from the beginning of the inductive phase to the end of the reproductive responsive phase

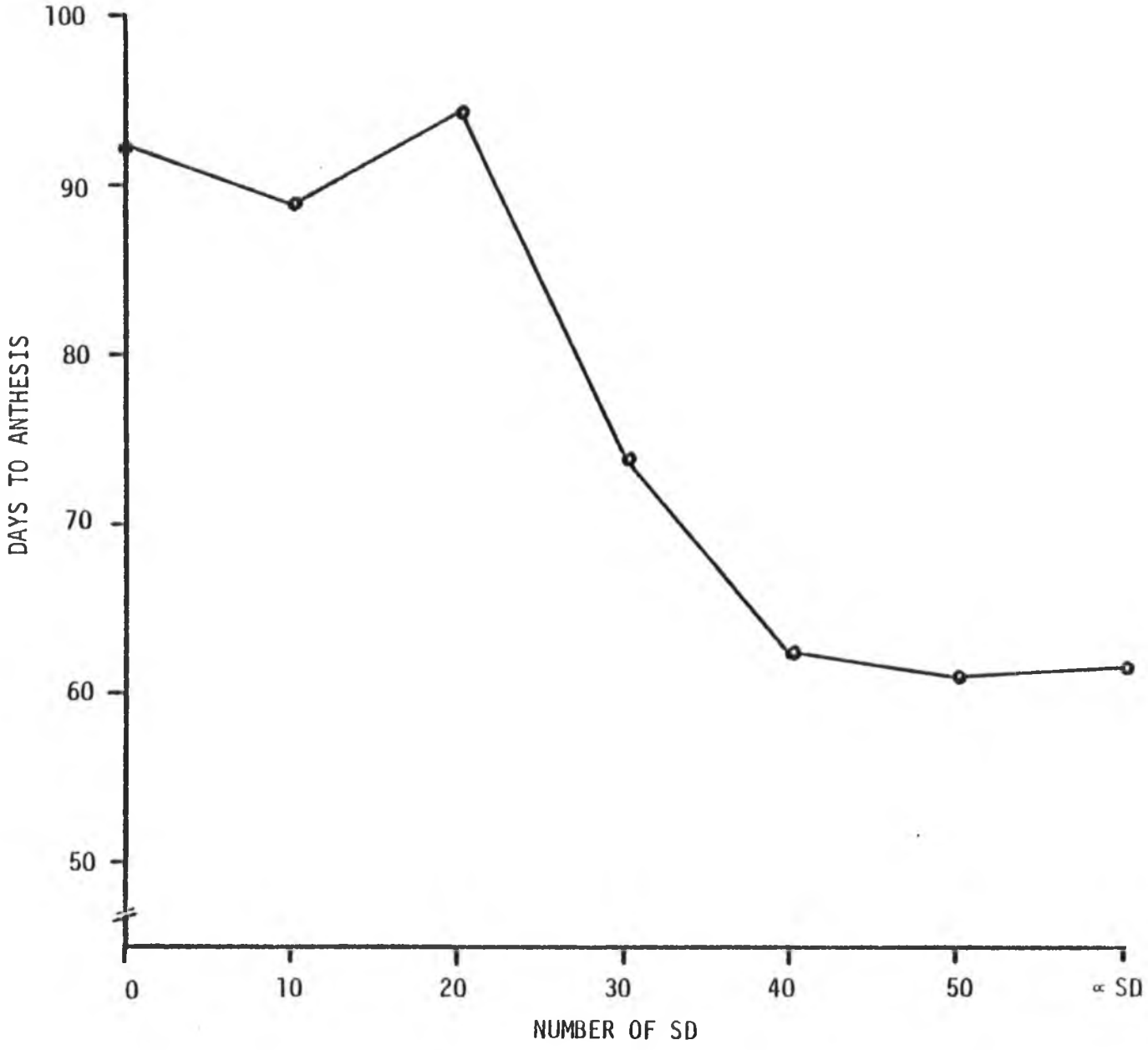

Figure 10. Effects of number of short-day (SD) exposure on days to anthesis in CM104 x Tx601

are necessary to promote earlier flowering in this sensitive hybrid.

4.4 Long-day Effects on Photoinduction

Growth Chamber Experiments:

The 3 genotypes used in the photoinduction experiments (Section 4.3) were also used to study the effects of long days on photoinduction. The mean DTI values are shown in Table 8. Analysis of variance of this experiment indicated there were highly significant sources of variation for genotypes, LD treatments and the interaction between LD and genotypes (Table 9). Using a 16 hour day to simulate the unfavorable photoperiodic days, it was generally found that for photoperiod sensitive genotypes, the longer the plants were kept under unfavorable daylength, the longer it would take to initiate its tassel. This retarding effect disappeared after 50 LD (from planting) in Tx601 and 40 LD in Va35 x Tx601. The long days were not effective in slowing down tassel initiation within the first 10 days in Tx601, and within the first 20 days in Va35 x Tx601. The DTI value of Va35 x Tx601 appeared to be intermediate between its component parental lines under 0 LD (or CSD) and CLD conditions.

In the photoperiod insensitive inbred Va35, minor but significant differences in DTI did occur among the different long day treatments. These could be discounted because of small sample size used in some of the samplings.

Greenhouse Experiments:

The photoperiod sensitive hybrid CM104 x Tx601 was subjected to long-day treatments of 0 LD, 10 LD, 20 LD, 30 LD, 40 LD, 50 LD, 60 LD, 70 LD, 80 LD, 90 LD and continuous LD followed by short-days. The experimental design was a randomized complete block with 3 replicates.

Table 8. Average days to tassel initiation of three genotypes exposed to short days after different periods of long day (LD) exposure

LD cycles	Va35	Tx601	Va35 x Tx601
0 LD	31.5	37.0	35.0
10 LD	34.0	36.0	34.0
20 LD	31.5	41.5	36.5
30 LD	36.0	45.5	40.5
40 LD	35.5	45.5	48.0
50 LD	34.5	59.0	49.0
CLD	36.0	60.0	50.0

Interaction BLSD (0.05) = 3.3

Table 9. Analysis of variance of data in Table 8

Source	d.f.	Mean Square
Rep	1	2.88
Genotype	2	176.67**
Error (a)	2	3.02
LD	6	207.43**
LD x Genotypes	12	43.46**
Error (b)	18	3.53

** Significant at 1%

It was generally found that increasing the number of long-day treatments for this hybrid, increased the length of time to flowering. The first 20 days (from the time of planting) under long days did not delay days to anthesis in CM104 x Tx601 significantly (Appendix 2). However, after 20 days, increasing the number of long days increased the delay (Figure 11). This levelled out after about 80 LD treatment, and further increases in long days made little difference to days to anthesis.

Exposing plants of CM104 x Tx601 to different number of long days in the greenhouse followed by short days revealed similar results as the growth chamber studies. As was discussed earlier, the juvenile phase in this hybrid was about 20 days. However, the upper limit estimate of the inductive phase was about 9 days under natural short days. The inductive phase was much longer under long days. The DTI value of CM104 x Tx601 under extended daylength in the field was found to average 46.7 days from planting. With a juvenile phase of 20 days, this would mean that the upper limit estimate for the inductive phase was about 27 days under long days. This was 3 times longer than that of the hybrid grown under short days. The inductive phase under long days could be shortened drastically on transfer to short days. Tassel development can also be speeded up if plants are subjected to short days after tassel initiation has occurred. This is indicated by the result for the 50 LD treatment in Appendix 2. Presumably tassel initiation had already occurred at the time of transfer to short days. The days to anthesis of this treatment as compared to that of the CLD treatment clearly confirms that daylength affects TI as well as tassel development. The reproductive responsive phase (from TI) in this case was estimated to be about 23 days under

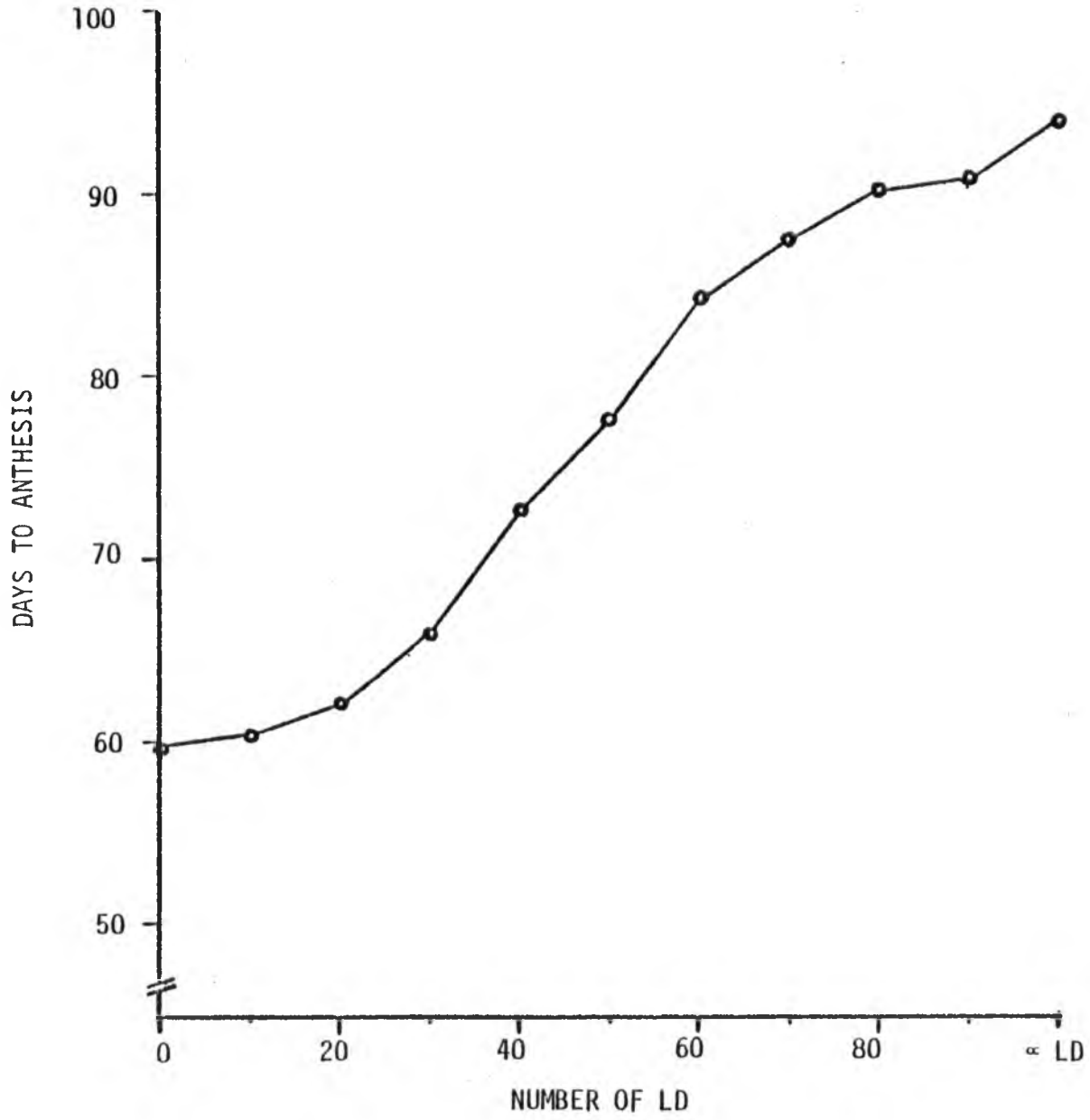

Figure 11. Effects of number of long-day (LD) exposure on days to anthesis in CM104 x Tx601

the long day conditions, since 70 LD was the last treatment which was significantly different from the CLD treatment. Compared to the estimated 11 days under short days, this was 2 times as long under long days.

4.5 Discussion

Tassel initiation is the first stage of the reproductive cycle of the corn plant, and this is frequently used in photoperiod response studies. Most studies have used Figure 2C of Bonnett's (1966) as the criterion of tassel initiation. In order to introduce a quantitative measure, Siemer, Leng and Bonnett (1969) suggested a meristem length of 0.4 mm to be taken as the stage of tassel initiation.

In screening for photoperiod insensitivity, the criterion used by Siemer et al. (1969) was adopted, and this was successful in identifying the sensitivity reaction of most genotypes studied. This screening revealed that genotypes from the tropics and subtropics were photoperiod sensitive, while genotypes from the temperate regions were much less sensitive. These were similarly reported by Arnold (1969b) and Spencer (1974).

The length of the developing tassel increases logarithmically with time after tassel initiation. This has also been noted in wheat and other grasses (Friend, 1965; Vince-Prue, 1975). Plotting tassel length from 0.4 mm and above on semi-log graph paper provides a useful technique to estimate tassel initiation time by extrapolation back to 0.4 mm. The highly significant correlation coefficients shown in Table 3 for the regression lines further supports the feasibility of using this technique. This will considerably reduce the drudgery of pinpointing the exact day in which a group of plants initiates their tassel. The accuracy of this

technique will depend on the number of plants dissected on each sampling date, as well as the number of sampling dates used for drawing the regression lines.

Stages of development can also be used in estimating the time of tassel initiation (Vince-Prue, 1975). The assignment of the various stages of development is usually arbitrary and often does not conform to any fixed standard. In addition, the number of days between any two stages of development can vary considerably, depending on how these stages are classified. The use of a quantitative measure such as tassel length instead of a subjective measure minimizes these discrepancies to a great extent.

Best (1960) in his paper on photoperiod response curves has described critical daylength as a certain threshold value of the photoperiodic reaction of a plant, and this is indicated by very great differences in time of floral initiation between two successive photoperiods. Critical daylength has also been defined by Vergara and Chang (1976) as the longest daylength at which the plant will flower or the daylength beyond which it will not flower. Francis (1972c) stated that the critical daylength for corn was between 14.5 and 15 hours. Although significant delays in tassel initiation were obtained between certain photoperiods in this study, these differences were not very great. Furthermore, these genotypes were known to flower in longer photoperiods than the ones studied here. According to Best (1960), when transitional forms of curves have been obtained between those for very low and for extremely high sensitivity to photoperiod in short-day plants, then to make a division somewhere in this fan of curves is an entirely arbitrary choice which is neither justified nor tenable.

Thus, he concluded that the existence of the many transitional forms of response curves did not justify the use of terms such as "quantitative and qualitative short (or long) day plants" and "the critical daylength." These forms of response curves were observed for corn in this study with varying degree of sensitivity types (Figure 8). Based on these observations, it may be concluded that critical daylength is not applicable in the genotypes studied.

Days to tassel initiation and leaf number are both affected by daylength (Table 4). DTI and leaf number both increase with increasing photoperiod for sensitive genotypes. These differences, however, are small and non-significant in photoperiod insensitive genotypes. The data imply that it is important to know the photoperiod sensitivity nature of the materials used in photoperiod studies or possibly even studies involving other aspects of light. Days to tassel initiation and emerged leaf number are highly correlated ($r = 0.96^{**}$). This relationship was also found by Aitken (1971, 1974, 1976) for grasses including corn. Several other researchers have also reported significant relationships between leaf number and maturity in corn (Chase and Nanda, 1967; Hesketh et al., 1969; Allen et al., 1973). Thus, leaf number can be used effectively in place of tassel initiation in screening for sensitivity differences to photoperiod. This has in fact, been used by Stevenson and Goodman (1972).

The effects of different number of short and long days on tassel initiation and flowering were well demonstrated for several genotypes in this study. Delayed tassel initiation in response to photoperiod changes were very distinct in photoperiod sensitive cultivars, but not so apparent

in photoperiod insensitive cultivars. The several studies conducted here thereby confirmed the insensitivity and sensitivity of Va35 and Tx601 respectively. Crosses between Va35 and Tx601 produced an F1 with intermediate sensitivity to photoperiod. This suggests that it is possible to narrow down the large sensitivity exhibited by exotic germplasm by crosses with photoperiod insensitive cultivars.

In the greenhouse experiment with CM104 x Tx601, the greater the number of short day cycles, the earlier anthesis would occur even if they were subsequently placed under the unfavorable long day cycles. This indicated the cumulative effects of induction. The first 20 days were not responsive to photoinduction as well as the long day inhibitory effects, and as such it could be attributed to the juvenile phase.

In subjecting plants to long days for different periods and transferring them to short days, it was found that long days had retarding or inhibitory effects on tassel initiation in photoperiod sensitive cultivars. This inhibitory effect of long days is of a certain duration and not cumulative, otherwise tassel initiation or flowering will not occur. As cited by Vergara and Chang (1976) the basic vegetative phase or the juvenile phase was measured by taking the duration of the vegetative growth phase at the optimum daylength. This measurement would have included the minimum number of photoinductive cycles. Thus in this case, the upper limit of the juvenile phase would be about 31.5, 37 and 35 days in Va35, Tx601 and their F1 respectively (Table 8). The results indicated that the inductive phase was longer (for Tx601 and Va35 x Tx601) under long than short days. However, TI was slightly earlier on transferring plants to short days before this phase was completed.

These series of studies involve only the tassel of the corn plant, but the photoperiod responses described here may possibly be the same in the developing ear shoots of corn. Effects of photoperiod in corn have not been investigated in depth and scope as in some plants. In view of its importance as a crop plant, more studies should be conducted.

5. PHOTOPERIOD EFFECTS ON AGRONOMIC CHARACTERS

5.1 10 x 10 Diallel Cross

The 10 entry diallel cross which consisted of parental lines with varying degrees of photoperiod sensitivity was planted under normal and extended daylength with three replicates at the Waimanalo Research Station. The design used was the strip block design with normal and extended daylengths arranged in strips. For most characters studied, highly significant mean squares (Table 10) were obtained for genotypes and interaction of daylength x genotypes; the only exception was the interaction for row number. There was no valid statistical test for the daylength treatments due to their arrangements in strips, although their mean squares were consistently very large for all characters.

Mean values of plant characters under both daylength regimes are presented in Table 11 for days to anthesis, Table 12 for silking and in Appendix 3 for plant and ear height. The 10 inbreds used in this study were previously classified in Table 2 of Section 4. These inbreds were Va35, B37 and Oh43 which were insensitive; A619, Hi25 and Mo17 which were intermediate; Hi26 and CM104 which were sensitive; and Hi30 and Tx601 which were highly sensitive to photoperiod. Hi26 was not as sensitive as it appeared to be in Table 2 and was misclassified as a result of no replication and small sample size used in the preliminary screening. For this entire study, Hi26 would be considered as intermediate. The intermediate grouping was sometimes referred to as low sensitivity (or moderately insensitive) in this study. Thus, for the convenience of discussing the results, the inbreds Va35, B37 and Oh43 were considered as insensitive; A619, Hi25, Hi26 and Mo17 were intermediate or low

Table 10. Mean squares of agronomic characters in the 10-entry diallel cross

Source	df	Days to anthesis	Days to silking	Plant height	Ear height	Cob length
Daylength (D)	1	21057.65	28443.21	45068.46	8616.99	282.45
Reps in D	4	73.73	93.66	1693.48	1580.86	20.22
Genotype (G)	54	205.81**	242.21**	3748.15**	3158.33**	38.54**
G x D	54	54.05**	54.45**	612.68**	418.38**	5.64**
Error (b)	216	2.27	3.17	115.03	48.83	1.34

Source	df	Filled ear length	Row no.	Kernels per row	Ear weight	Grain weight	100 kernel weight	Kernel depth
Daylength (D)	1	77.00	2.67	52.80	1809.29	11.55	644.28	0.1624
Reps in D	4	9.81	0.86	57.71	5406.27	15.58	26.30	0.0065
Genotype (G)	54	49.92**	12.79**	368.81**	19952.99**	52.88**	103.10**	0.0490**
G x D	54	9.16**	6.23	51.21**	2161.01**	6.48**	23.28**	0.0195**
Error (b)	216	1.50	5.37	11.81	527.81	1.51	5.90	0.0032

Table 11. Days to anthesis of the 10-entry diallel cross under normal and extended daylength

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601	Array Mean
Va35	57.6[a]	55.0	57.0	56.0	56.0	58.5	56.4	55.7	58.3	61.2	57.2
	67.0	66.2	69.3	68.1	66.7	68.2	71.2	71.2	74.3	83.0	70.5
A619		56.4	55.2	54.5	54.7	56.9	56.3	55.3	58.3	61.1	56.4
		68.8	66.1	67.8	64.6	68.8	68.9	71.5	77.3	78.4	69.8
B37			59.5	55.2	55.8	57.3	59.8	57.3	59.7	62.1	57.9
			71.3	67.1	66.0	68.3	71.6	72.6	79.6	79.8	71.2
Oh43				56.2	55.3	54.8	57.2	56.5	58.2	59.0	56.3
				70.7	66.5	66.2	71.1	71.9	77.8	78.9	70.6
Mo17					57.7	56.8	57.7	55.5	58.7	59.3	56.8
					72.3	68.8	71.4	70.6	78.1	79.1	70.4
Hi25						62.0	57.8	57.5	59.2	60.8	58.2
						73.7	71.2	75.0	75.8	82.6	71.9
Hi26							60.7	58.5	60.0	64.1	58.8
							77.0	72.2	77.8	81.7	73.4
Hi30								58.4	58.9	60.4	57.4
								77.2	76.0	85.5	74.4
CM104									64.3	66.2	60.2
									96.8	93.0	80.6
Tx601										71.9	62.6
										116.4	85.8

[a] Upper and lower values represent normal and extended daylength respectively.
Interaction BLSD (0.05) = 2.5

Table 12. Days to silking of the 10-entry diallel cross under normal and extended daylength

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM109	Tx601	Array Mean
Va35	58.6[a]	55.2	57.0	56.6	57.2	59.9	57.9	57.0	59.5	61.9	58.1
	70.2	70.3	72.3	71.7	70.3	71.9	75.1	76.3	77.7	87.4	74.3
A619		58.0	55.2	55.5	55.4	58.2	57.7	57.0	59.3	62.3	57.4
		75.7	69.0	73.5	67.1	72.1	72.8	76.7	82.0	81.7	74.1
B37			62.4	55.0	57.7	58.1	61.4	58.7	61.4	63.2	59.0
			75.3	69.1	70.5	70.8	76.1	76.7	84.6	82.2	74.7
Oh43				56.9	55.8	55.1	58.7	57.3	59.4	60.0	57.0
				74.2	68.8	70.6	74.9	75.4	81.4	81.4	74.1
Mo17					60.5	57.8	61.4	60.0	60.6	61.8	58.8
					78.9	72.1	75.6	76.0	83.8	83.3	74.6
Hi25						64.7	60.5	59.0	61.3	62.4	59.7
						78.9	74.7	80.1	78.9	85.9	75.6
Hi26							63.7	61.4	62.5	66.5	61.2
							81.8	76.6	82.1	85.0	77.5
Hi30								61.3	61.2	62.6	59.6
								84.6	81.5	92.5	79.6
CM104									67.0	68.7	62.1
									102.4	99.6	85.4
Tx601										76.2	64.6
										120.6	90.0

[a] Upper and lower values represent normal and extended daylength respectively.
Interaction BLSD (0.05) = 3.0

sensitivity; and Hi30, CM104 and Tx601 were considered as sensitive to photoperiod.

Days to anthesis and silking were delayed significantly under extended daylength irregardless of the nature of the genotypes. However the magnitude of this delay differed, with photoperiod sensitive genotypes (Hi30, CM104 and Tx601) having the greatest delay followed by crosses of insensitive x sensitive and intermediate x genotypes, and then with relatively smaller delay in photoperiod insensitive genotypes. The delays in anthesis and silking appeared to be larger than expected for the insensitive inbreds such as Va35, B37 and Oh43 (as classified in Section 4). This could be attributed to phosphorus stress for the plants grown under extended daylength which showed symptoms of phosphorus deficiency at the early stages of growth. In addition, a heavy thunderstorm at that same period had subjected this area to temporary waterlogging. These joint mishaps might have caused an additional delay of a few days to anthesis and silking. This would explain why the insensitive genotypes experienced such a big difference in these characters.

In the case of plant and ear height, there were significant increases in height with photoperiod sensitive genotypes involving Hi30, CM104, Tx601 and their crosses. Hybrids involving these sensitive inbreds in crosses with insensitive or intermediate inbreds were also found to have significant increases in height under extended daylength, but of a lesser magnitude than the sensitive genotypes. In the case of insensitive and intermediate genotypes and their crosses, extended daylength did not bring about significant increase in plant and ear height although exceptions did occur. Extended daylength did not appear to cause a significant

increase in plant height of Tx601 (Appendix 3). This was because late maize mosaic virus infection caused partial stunting of all plants of this genotype.

Grain yield data of the 10 entry diallel under the two daylength regimes are presented in Table 13. Generally, inbreds which were insensitive or intermediate to photoperiod as well as their hybrids had lower yields under extended daylength. On the contrary, crosses between insensitive or intermediate and sensitive inbreds had slightly higher yields under extended daylength than under normal daylength, although few of these differences were significant. The yields of CM104, Tx601 as well as their hybrid were extremely poor under the extended daylength. With the added light, the yield of Tx601 was very close to zero.

As a result of delayed flowering, the sensitive genotypes had a long growing period under extended daylength, and as such diseases and pests have a greater opportunity to decimate the crop. This was the primary reason for the low yield in CM104, Tx601 and their hybrid. In fact they were heavily infested with stalk rot and maize mosaic virus. Another reason for the low yield was the poor pollination obtained in this evaluation. Most of the neighboring plants had shed their pollen long before these plants came into flower. Furthermore, delay in silking as compared to anthesis may also account for the poor pollination of these sensitive genotypes under long day conditions. Because Hi30 was not as highly sensitive as CM104 and Tx601, this inbred as well as its crosses with the highly sensitive inbreds CM104 and Tx601 flowered relatively earlier and thus did not suffer the same fate as CM104, Tx601, and CM104 x Tx601.

Table 13. Grain yield (metric tons/ha) of the 10-entry diallel cross under normal and extended daylength

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601	Array Mean
Va35	3.96[a]	5.85	8.25	5.15	8.10	7.46	7.05	8.44	10.22	11.67	7.62
	2.97	4.56	5.39	4.21	7.09	9.20	5.10	9.50	12.01	9.51	6.95
A619		3.35	7.91	4.80	8.86	6.95	9.82	9.01	10.74	13.70	8.10
		2.17	5.66	1.90	8.36	7.22	8.57	10.48	13.03	13.23	7.52
B37			3.36	7.45	7.98	7.28	9.75	9.97	10.90	11.52	8.44
			2.82	6.66	7.38	5.96	9.19	8.68	9.48	10.46	7.17
Oh43				3.59	8.20	9.29	9.62	9.17	11.88	11.11	8.03
				3.44	8.56	7.62	9.51	11.75	14.43	12.14	8.02
Mo17					5.08	7.66	10.67	6.93	10.98	10.70	8.52
					5.09	9.24	10.64	9.64	12.04	9.21	8.72
Hi25						3.14	7.93	8.73	10.83	9.35	7.86
						2.40	8.39	10.05	10.72	12.39	8.32
Hi26							6.00	10.52	11.87	10.92	9.42
							4.27	12.11	12.05	12.44	9.23
Hi30								5.22	10.69	10.78	8.95
								5.77	11.46	12.30	10.17
CM104									8.38	10.60	10.71
									1.67	2.39	9.93
Tx601										3.78	10.41
										0.00	9.41

[a] Upper and lower values represent normal and extended daylength respectively.

Interaction BLSD (0.05) = 1.99 Mean heterosis = 105.77% (Normal daylength)
250.17% (Extended daylength)

The highest yielding hybrid under the normal daylength of Hawaii was A619 x Tx601. In addition its yield was relatively stable even under extended daylength. The hybrids Mo17 x Hi30 and Hi25 x Tx601 showed the highest percentage gain in grain yield under the extended daylength. Generally, grain yield of temperate genotypes was below that of tropical genotypes under normal as well as extended daylength in Hawaii. Heterosis percentage under extended daylength was much higher (250.17%) than that under normal daylength (105.77%). This was attributed to the poor yielding capacity of the temperate inbreds as well as the extremely poor yield under the extended daylength.

In examining the yield components under normal and extended daylength, it was found that generally cob length (Table 14) and filled ear length (Table 15) increased significantly under extended daylength with genotypes of insensitive x sensitive and intermediate x sensitive background. With very sensitive inbreds, CM104 and Tx601 and their hybrid, cob length decreased and only significantly in Tx601. Filled ear length was drastically reduced under extended daylength. The yield reduction was the result of diseases as mentioned earlier, and not as a direct result of photoperiod. This would be obvious when the results on kernel initials per row are discussed. Insensitive and intermediate genotypes exhibited longer cob length in most cases under extended daylength, although not all were significantly different. With filled ear length, genotypes of the intermediate grouping, i.e. crosses among Mo17, Hi25 and Hi26 showed increases under extended daylength with some having significant differences. With insensitive genotypes, there were generally no significant differences in filled ear length.

Table 14. Cob length of the 10-entry diallel cross under normal and extended daylength

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601	Array Mean
Va35	12.7[a]	14.7	15.8	14.1	17.6	16.9	16.3	16.5	18.1	18.0	16.1
	12.3	14.1	16.3	15.1	19.6	20.4	15.8	20.3	23.3	20.0	17.7
A619		11.7	15.4	13.6	17.8	15.8	16.6	15.9	18.0	19.2	15.9
		12.3	14.8	11.5	19.2	18.4	17.3	20.0	23.6	21.8	17.3
B37			12.5	16.6	17.7	15.6	17.1	18.1	17.3	18.0	16.4
			13.3	17.1	19.1	17.0	19.6	19.8	19.5	20.2	17.7
Oh43				13.0	17.4	16.8	16.1	16.2	18.2	17.1	15.9
				13.3	19.1	16.9	18.3	19.3	21.6	19.3	17.2
Mo17					15.3	17.5	19.1	15.8	18.1	18.0	17.4
					18.9	19.7	21.4	20.4	24.2	20.0	20.2
Hi25						13.6	16.4	17.0	18.4	17.5	16.6
						12.9	18.0	19.7	20.4	21.4	18.5
Hi26							14.2	17.7	18.9	17.1	17.0
							15.1	20.8	22.0	20.3	18.9
Hi30								13.5	17.5	16.8	16.5
								17.4	20.9	19.6	19.8
CM104									16.2	17.6	17.8
									15.8	16.8	20.8
Tx601										11.7	17.1
										7.2	18.7

[a] Upper and lower values represent normal and extended daylength respectively.
Interaction BLSD (0.05) = 2.0

Table 15. Filled ear length of the 10-entry diallel cross under normal and extended daylength

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601	Array Mean
Va35	10.4[a]	12.8	13.2	12.1	15.6	14.6	13.6	14.3	16.2	16.9	14.0
	9.9	11.8	12.5	13.0	15.9	17.4	12.7	17.2	19.0	17.7	14.7
A619		9.2	13.6	11.5	15.4	12.1	14.8	13.5	15.3	17.3	13.6
		9.3	12.3	8.7	17.1	14.7	15.0	16.8	19.8	19.3	14.5
B37			10.1	14.5	15.8	13.2	15.4	16.1	15.4	16.8	14.4
			9.9	13.6	16.4	14.1	17.5	16.6	15.7	17.2	14.6
Oh43				11.4	15.7	13.8	14.2	14.6	16.7	15.4	14.0
				10.8	17.7	14.9	16.6	17.4	18.6	17.3	14.9
Mo17					13.5	15.5	17.5	13.6	16.2	16.6	15.5
					16.2	17.8	20.0	18.1	19.5	18.1	17.7
Hi25						10.6	14.2	14.3	16.3	15.7	14.0
						9.8	15.7	17.1	17.7	18.2	15.7
Hi26							11.4	15.6	17.3	15.6	15.0
							12.7	18.6	18.4	18.8	16.6
Hi30								10.6	15.5	15.2	14.3
								14.0	17.8	17.9	17.2
CM104									13.8	15.8	15.8
									7.6	8.9	16.3
Tx601										8.0	15.3
										0.1	15.4

[a] Upper and lower values represent normal and extended daylength respectively.
Interaction BLSD (0.05) = 1.9

With the exception of Tx601, row number of all genotypes was unaffected by additional daylength (Appendix 4).

Kernels per row (Appendix 4) appeared to decrease slightly under extended daylength among insensitive and intermediate genotypes, and to increase slightly among insensitive x sensitive or intermediate x sensitive hybrids. These were however not significant in most cases, as a result of a large estimate of BLSD. This was due to the large variation caused by the significant reduction in kernels per row for the highly sensitive genotypes.

The 100 kernel weights were lower under extended than normal daylength among insensitive genotypes with few exceptions. There was no clear-cut trend in the crosses of insensitive x sensitive and intermediate x sensitive genotypes for this character with some genotypes increasing and some decreasing with the added light. Most of the sensitive inbreds and their crosses had significant reductions in kernel weight under extended light due to the problems mentioned previously.

Kernel depths were little affected by additional light (Appendix 4). Generally, it was slightly reduced under extended daylength, but slightly higher in a few cases involving insensitive x sensitive, and intermediate x sensitive crosses. Significant reduction in kernel depth occurred for the highly sensitive inbreds CM104, Tx601 and their hybrid, as noted previously.

5.2 5 x 5 Diallel Cross

A 5 entry diallel cross was extracted from the preceding 10 entry diallel to study the additional characters of tassel initiation (DTI), leaf number, days for tassel development (DTD) and kernel initials per

row. Analyses of variance of these data (Table 16) indicated that highly significant variation occurred among genotypes as well as the interaction of genotypes with daylength. As described earlier, there was no valid test for daylength effects in this experiment.

DTI was significantly greater under extended daylength (Table 17), with high genotype x daylength interactions. The delay in tassel initiation was lower among those genotypes involving inbreds Va35, B37 and Oh43 which were insensitive to photoperiod as compared to their crosses with sensitive inbreds CM104 and Tx601. The delay in DTI was greatest among the sensitive genotypes (i.e. CM104, Tx601 and their F_1).

The period from tassel initiation to anthesis, or days for tassel development (DTD), was also significantly increased by extended daylength for essentially all genotypes (Table 18). The magnitude of delay was more or less the same among most genotypes. It tended to be slightly larger with sensitive genotypes, especially the inbred Tx601. The disease problems associated with the sensitive inbreds would probably have affected the DTD values greatly by its effects on the tassel and the ear shoot.

In comparing the delays associated with DTI and DTD under extended daylength (Table 19), it was generally found that the longer photoperiod affected tassel initiation time more than the period from tassel initiation to anthesis. The degree of these effects varied with the genotypes. The ratio of DTI/DTD delays would indicate the proportionate effect of long days on DTI and DTD. The ratio ranged from 0.61 to 3.72 in the 5-entry diallel (Table 19) with the mean of 2.24. Thus, long days in general would delay tassel initiation twice as much as tassel development.

In the case of leaf number measurements (Table 20), extended daylength

Table 16. Mean squares of some characters studied in the 5-entry diallel cross

Source	df	DTI	Leaf no.	DTD	Kernel initials/row
Daylength (D)	1	3648.10	302.50	991.35	963.67
Reps in D	4	24.46	0.62	4.04	3.60
Genotype (G)	14	198.02**	83.65**	72.99**	133.44**
G x D	14	49.38**	10.32**	30.46**	21.30**
Error (b)	56	3.93	0.28	3.74	4.54

Table 17. Days to tassel initiation of the 5-entry cross under normal and extended daylength

	Va35	B37	Oh43	CM104	Tx601	Array mean
Va35	24.0[a]	22.3	21.0	21.3	23.3	22.4
	28.0	27.0	29.3	33.7	40.3	31.7
B37		22.3	21.7	23.7	24.5	22.9
		30.7	31.0	36.0	37.7	32.5
Oh43			22.7	22.7	24.0	22.4
			33.3	37.3	36.3	33.4
CM104				28.0	29.0	24.9
				50.7	46.7	40.9
Tx601					32.7	26.7
					56.3	43.5

[a] Upper and lower values represent normal and extended daylength respectively.

Interaction BLSD (0.05) = 3.1

Table 18. Days for tassel development of the 5-entry diallel cross under normal and extended daylength

	Va35	B37	Oh43	CM104	Tx601	Array mean
Va35	33.6[a]	34.6	34.9	37.0	37.9	35.6
	39.0	42.3	38.8	40.7	42.7	40.7
B37		37.2	33.6	36.0	37.4	35.8
		40.6	36.1	43.6	42.1	40.9
Oh43			33.6	35.5	35.0	34.5
			37.4	40.5	42.6	39.1
CM104				36.3	37.2	36.4
				46.1	46.3	43.4
Tx601					39.2	37.3
					60.0	46.7

[a]Upper and lower values represent normal and extended daylength respectively.

Interaction BLSD (0.05) = 2.8

Table 19. Comparative delays in DTI and DTD under extended daylength in the 5-entry diallel cross

Genotypes	DTI	DTD	DTI/DTD
Va35	4.0	5.3	0.75
B37	8.3	3.4	2.44
Oh43	10.7	3.8	2.82
CM104	22.7	9.8	2.32
Tx601	23.7	20.8	1.14
Va35 x B37	4.7	7.7	0.61
Va35 x Oh43	7.7	3.8	2.03
Va35 x CM104	12.3	3.7	3.32
Va35 x Tx601	17.0	4.8	3.54
B37 x Oh43	9.3	2.5	3.72
B37 x CM104	12.3	7.6	1.62
B37 x Tx601	13.0	4.7	2.77
Oh43 x CM104	14.7	4.9	3.00
Oh43 x Tx601	12.3	7.5	1.64
CM104 x Tx601	17.7	9.1	1.94
Average	12.7	6.6	2.24

Table 20. Leaf number of the 5-entry diallel cross under normal and extended daylength

	Va35	B37	Oh43	CM104	Tx601	Array mean
Va35	14.8[a]	15.3	14.8	17.1	18.7	16.1
	15.1	16.1	16.0	20.0	22.6	18.0
B37		14.9	15.3	17.2	18.5	16.2
		16.4	16.9	20.6	22.3	18.5
Oh43			14.3	17.0	18.1	15.9
			17.1	21.5	23.2	18.9
CM104				19.6	20.8	18.3
				26.3	27.8	23.2
Tx601					22.7	19.8
					32.4	25.7

[a] Upper and lower values represent normal and extended daylength respectively.

Interaction BLSD (0.05) = 0.8

significantly increased leaf number for all genotypes except the photoperiod insensitive inbred Va35. The magnitude of the increase in leaf number depended on the photoperiod sensitivity and was similar to that described for DTI.

The number of kernel initials per row increased significantly under extended daylength for all genotypes except Va35 and B37 x CM104 which were not significant (Table 21). The increase was greatest for the sensitive genotypes CM104, Tx601 and their hybrid.

Using the data from the 5-entry diallel cross under normal and extended daylengths, correlation coefficients were computed among the following characters: DTI, leaf number, DTD, days to anthesis and days to silking. It was found that all these characters were highly correlated with one another (Table 22). Similarly using only the difference between the effects of extended daylength and normal daylength (i.e. photoperiod sensitivity) for each character, a correlation matrix was set up (Table 23). Although all correlation coefficients were highly significant, the correlation of DTD with DTI was considerably lower.

5.3 Discussion

In accordance with the results of many workers, long day conditions delayed anthesis and silking in corn. This delay was especially great for photoperiod sensitive genotypes. With photoperiod insensitive genotypes, such delays were of a much lesser magnitude, suggesting that all genotypes have some sensitivity to photoperiod but of different degrees. Plants under extended daylength experienced phosphorus stress at the early stages of growth. This might have influenced some of the conclusions in this study. In growth chamber studies (Section 4), days

Table 21. Kernel initials per row of the 5-entry diallel cross under normal and extended daylength

	Va35	B37	Oh43	CM104	Tx601	Array mean
Va35	47.8[a]	51.3	49.0	54.0	57.6	51.9
	48.8	58.9	54.8	62.0	64.9	57.9
B37		49.3	53.2	54.5	55.9	52.8
		53.2	57.3	57.3	65.1	58.4
Oh43			44.5	52.2	53.7	50.5
			48.4	55.8	57.9	54.8
CM104				41.6	52.4	50.9
				54.5	61.8	58.3
Tx601					40.2	52.0
					54.4	60.8

[a]Upper and lower values represent normal and extended daylength respectively.

Interaction BLSD (0.05) = 3.3

Table 22. Correlation coefficients of several characters based on data from the 5-entry diallel cross

	Leaf no.	DTD	Days to anthesis	Days to silking
DTI	0.885**	0.809**	0.973**	0.973**
Leaf no.		0.824**	0.904**	0.894**
DTD			0.923**	0.910**
Days to anthesis				0.995**

** Significant at 1% level

Table 23. Correlation coefficients of several characters based on photoperiod sensitivity from the 5 x 5 diallel cross

	Leaf no.	DTD	Days to anthesis	Days to silking
DTI	0.898**	0.491**	0.895**	0.900**
Leaf no.		0.713**	0.943**	0.926**
DTD			0.827**	0.781**
Days to anthesis				0.980**

** Significant at 1% level

to tassel initiation for the insensitive genotypes showed smaller photoperiod sensitivity as compared to the results obtained for days to tassel initiation, anthesis, and silking in this study.

Delay in flowering can be attributed to the joint effects of long days delaying tassel initiation time and the period from tassel initiation to anthesis and silking. Breuer et al., 1976 reported that photoperiod did not affect the latter stage. However this study as well as that of Faungfupong (1976) and Aitken (1977) appear to have found otherwise. Both Faungfupong and Aitken have stated that there was a much greater delay for silking than tasseling or anthesis. This was also found to be so for all genotypes used in this study. However, the delay was at the most a week and was not as great as that reported by Aitken (1977) for Puna, a Peruvian highland variety, planted in temperate southern Australia. This study also confirms the results presented in Section 4 that daylength had a greater influence on tassel initiation time than on the duration of tassel development.

There was not too much of a difference in days to anthesis and days to silking among the genotypes under the normal daylength of Hawaii as compared to the differences generated by the extended daylength. The daylength variation of 10.8 to 13.4 hours (sunrise to sunset) in Hawaii would not be sufficient to cause any major delay in flowering. This has been termed a neutral environment by Brewbaker (1974). Under these conditions, flowering in corn plants can be considered to be a function of maturity. However, under long day conditions, flowering is a complex confounding of maturity and photoperiod sensitivity.

As a result of delayed tassel initiation and flowering, there is a longer period of vegetative growth with more leaves being produced and

consequently the plant is much taller. This is very apparent in the photoperiod sensitive genotypes. Other workers have also reported an increase in leaf number under long day conditions (Hesketh et al., 1969; Stevenson and Goodman, 1972; Hunter et al., 1974; Spencer, 1974; Coligado and Brown, 1975a). In addition, ear height also increased under extended daylength as has been reported by McClelland (1928), Urano et al. (1959), and Chaudhry (1968). The magnitude of the increases in leaf number, plant height and ear height under long days depended on the nature of the photoperiod sensitivity for the genotypes. Generally, such increases in these characters increased with increased sensitivity to long days. This is in agreement with the results of Spencer (1974).

Little has been published on the effects of photoperiod on grain yield and yield components in corn, except the work of Ragland et al. (1966). As the results here showed, there is an interesting trend in the effects of extended daylength on grain yield and yield components depending on the sensitivity nature of the genotypes. This will be discussed under 3 groupings, i.e. insensitive, sensitive, and insensitive x sensitive. Unfortunately, in some literature on photoperiod response there is a failure to establish the photoperiod sensitivity of the genotypes studied.

Grain yield of the photoperiod insensitive genotypes was reduced under extended daylength. Ragland et al. (1966) reported similar results with C103 x B37. Although the photoperiod sensitivity was not described, this hybrid presumably is insensitive, since C103 is in the pedigree of Va35 (an insensitive inbred), and B37 is also insensitive. The reduction in grain yield of the insensitive genotypes can best be related to the effects of photoperiod on the yield components. Counts of kernel initials

per row from the 5 x 5 diallel cross as well as cob length measurements have indicated that there is a potential for higher yield for this group of genotypes under long days. On the contrary, filled ear length was reduced, although some of the intermediate or weakly insensitive types showed an increase. However, in the case of kernels per row, there was generally a slight reduction indicating that the number of kernels filled were far below its potential. It might be possible that part of the unfilled earlength was already pollinated but failed to develop into mature kernels as suggested by Ragland et al. (1966). The 100 kernel weight was also lighter and kernel depth smaller under extended daylength. Thus the reduced grain yield of the insensitive genotypes may be attributed to fewer mature kernels per row, smaller kernel size and reduced weight per kernel. This conclusion was also obtained by Ragland et al. (1966).

The use of supplementary light causes plants to develop longer cob lengths, and more kernel initials per row for the insensitive genotypes. This larger "sink" for photosynthates is apparently not filled because the short period of vegetative growth is not sufficient to accumulate the photosynthates necessary to make full use of the larger "sink." The long duration of high intensity sunlight together with the longer photoperiod may partly account for the higher corn yields typical of the Corn Belt as compared to the tropics.

The disease problems as well as poor pollination in the sensitive genotypes under the extended daylength greatly affected grain yield as a result of a delay in flowering. This drastic effect resulted in zero yield for Tx601, the most sensitive inbred. Hi30, which was less sensitive than Tx601 and CM104 and its crosses with these two highly sensitive

inbreds were found to have yield increases in contrast to the results of the strongly sensitive genotypes. Sensitive genotypes as a whole have the highest increase in the kernel initials per row under extended daylength. However, this advantage is negated by the stalk rot and maize mosaic infections.

Faungfupong (1976) also found that use of supplementary light with the long days of Iowa had an adverse effect on grain yield. However there was no mention of the genotypes used and as such it was not sure whether the materials he used were sensitive to photoperiod or not. Hunter et al. (1977), however, reported that longer photoperiod favored increased grain yield in the hybrid Harrow 691, which was previously reported to be photoperiod sensitive (Hunter et al., 1974). Since their studies were conducted in controlled growth cabinets, there is no basis for comparison with the low yield obtained by the photoperiod sensitive materials studied here. Furthermore, Harrow 691 is a hybrid adapted to southwestern Ontario (Hunter et al., 1974) and cannot be as sensitive as the tropical materials studied here.

In the crosses between insensitive and sensitive inbreds, higher yield was obtained under extended than normal daylength. This group of genotypes were still sensitive to photoperiod but of an intermediate magnitude between their component parental inbreds. Thus under extended daylength, they did not flower as late as their sensitive parental lines and therefore, were able to exploit to good advantage the slightly longer growing period. By virtue of the photoperiod effects, kernel initials per row were increased leading to significant increases in cob length as well as filled ear length. Unlike the insensitive group, this group of genotypes were able to accumulate more photosynthate into the larger

"sink" since they had a slightly longer growing period as well as slightly more leaves to manufacture photosynthates.

It therefore appeared that insensitive x sensitive genotypes would have tremendous yielding capacity under the long days of the Corn Belt. However, one must consider the magnitude of the delay in flowering. It would be certain that any significant delay in flowering would not be advantageous in the Corn Belt. Furthermore in some instances the first cross between the insensitive and sensitive genotypes carry along with it some unusual growth responses that are observed with the sensitive genotypes under long day conditions. These are the increased rings of brace roots formed (Figure 12) as well as occasional tassel tippings in the ear shoots (Figure 13). In addition, incomplete husk covers (Figure 14) were also observed in some cases. This was due to longer ears under extended daylength with possibly no daylength effects in lengthening the husks at the same time. Nevertheless, if a conversion program were to be carried out to convert sensitive genotypes for adaptation in the Corn Belt, a little sensitivity should be retained to take advantage of the beneficial photoperiod effects. The amount of delay due to this sensitivity must not be excessive in view of the fact that the growing season is limited only to the summer months. In addition, the economical aspects of a slightly longer growing period must also be taken into consideration. More studies have to be carried out with the above problems in mind. Thus sensitivity to photoperiod remains to be exploited, not to mention of the increased genetic diversity associated with the exotic tropical genotypes.

In the tropics, it is definitely not advantageous and practical to set up lights to extend the short daylength for the extra yield. It is

Figure 12. Excessive brace root formation associated with photoperiod sensitivity under extended daylength

Figure 13. Tassel tipping of photoperiod sensitive genotypes under extended daylength

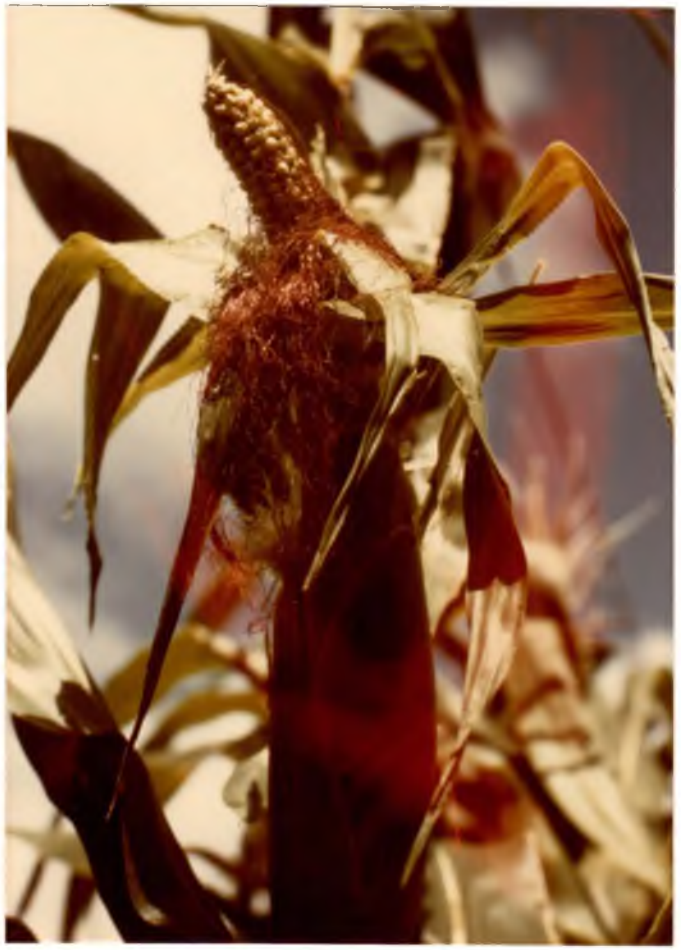

Figure 14. Incomplete husk cover due to longer ears of photoperiod sensitive genotypes under extended daylength

not certain whether night interruptions by a short flash of light will bring about the same effects, although it delays flowering of most short-day plants. However, there may be other ways of delaying tassel initiation or flowering to extend the length of the growing period, such as the use of growth regulators. Defoliating young seedling plants by means of clipping will also delay flowering as demonstrated by Cloninger et al. (1974) and Hicks et al. (1977). Hicks et al. (1977) have demonstrated that clipping a short season hybrid at the 5 leaf stage in Minnesota caused an average increase of 48% in grain yield compared to no defoliation. With a full season hybrid, the same treatment caused a 7% yield reduction. This seemed to be analogous to the effects of photoperiod. However, more work has to be carried out to ascertain the value of delayed flowering by chemical means or by clipping seedlings in the tropics.

Days to tassel initiation is highly correlated with leaf number, days for tassel development, days to anthesis and days to silking. These results disproved the earlier findings of Leng (1951) who found no correlation between earliness and days to tassel initiation, and between days to tassel initiation and tassel development. At the same time, leaf number was also found to be highly correlated with days to anthesis and silking. This is in agreement with the findings of many other workers including Chase and Nanda (1967), Allen et al. (1973) and Bonaparte and Brown (1976).

Days to tassel initiation is the first stage of tassel differentiation and as such has often been used in photoperiod response studies. The determination of DTI involves destructive sampling and this is impractical to a plant breeder not to mention of the tedious and laborious dissections involved. Aitken (1976) has proposed a non-destructive method

to estimate tassel initiation based on the high correlation between tassel initiation time and the leaf number at that time. However, using the photoperiod sensitivity of days to tassel initiation, it was found here that DTI was highly correlated with the sensitivity expressed in leaf number, days to anthesis and days to silking. Thus, for the purpose of the plant breeder, the use of leaf number, days to anthesis or days to silking will serve as good criteria as tassel initiation in studying or isolating photoperiod insensitivity in corn. In addition to cutting down the amount of work, these characters have also an added advantage of being non-destructive.

6. GENETICS OF PHOTOPERIOD SENSITIVITY

6.1 5 x 5 Diallel Analysis

Five parental lines, of which three were insensitive temperate inbreds (Va35, B37 and Oh43) and two were sensitive tropical inbreds (CM104 and Tx601) were chosen as a 5 entry diallel cross, extracted from the 10 entry diallel. As described in Section 5, they were evaluated under normal and extended daylengths at the Waimanalo Research Station. Sensitivity index was computed by calculating the difference in days between the extended and normal daylength data in the characters used for assessing photoperiod sensitivity. The characters used were days to tassel initiation and leaf number. Analyses of variance of these data (Table 24) showed highly significant genotypic differences for photoperiod sensitivity. Since genotypic differences existed, they were subjected to the diallel analysis using Griffings' Method 2 - Model 1.

Mean squares for general combining ability (GCA) were highly significant in the characters studied (Table 25). Specific combining ability (SCA) mean squares were significant at 5% for days to tassel initiation but non-significant for leaf number. The GCA/SCA ratios were very high.

Photoperiod sensitivity (i.e. the difference in values of normal and extended daylength) for days to tassel initiation in a 5 entry diallel cross are presented in Table 26. Va35 showed the lowest sensitivity and CM104 (a Cuban Flint derived inbred) and Tx601 (a Tuxpeno derived inbred) showed very high sensitivity to photoperiod. Crosses among the insensitive temperate inbreds showed low sensitivity. In crosses between the temperate and tropical inbreds, photoperiod sensitivity was approximately intermediate between the parental values. In comparing the sensitivity

Table 24. Analysis of variance of photoperiod sensitivity expressed in DTI and leaf number in a 5-entry diallel cross

Source	df	Mean squares	
		DTI	Leaf no.
Replicate	2	24.42*	3.56*
Genotypes	14	100.12**	288.87**
Error	28	6.61	14.63

Table 25. Mean squares for general and specific combining abilities and error of photoperiod sensitivity expressed in DTI and leaf number

Characters	GCA	SCA	GCA/SCA	Error
Days to tassel initiation	102.94**	5.54*	18.58	2.20
Leaf number	23.16**	0.36	64.33	0.17

Table 26. Photoperiod sensitivity expressed in days to tassel initiation and its GCA effects in a 5-entry diallel cross

	Va35	B37	Oh43	CM104	Tx601	GCA Effects
Va35	4.0	4.7	7.7	12.3	17.0	-3.78
B37		8.3	9.3	12.3	13.0	-2.88
Oh43			10.7	14.7	12.3	-1.54
CM104				22.7	17.7	3.74
Tx601					23.7	4.46

BLSD (0.05) = 3.7

S.E. (gi - gj) = 0.79

Mean heterosis % = -10.96%

data of the insensitive inbreds in Table 26 with that of the growth chamber studies (Section 4), the sensitivity expressed in DTI from the field evaluation was somewhat slightly higher. A number of environmental factors absent in controlled growth chambers could have caused this overestimate. As described earlier in Section 5, the field under the extended daylength was waterlogged temporary at the early stage of growth after a thunderstorm. At the same time, phosphorus stress was evident with distinct purple coloration symptoms. The coefficient of linear determination between parental means and GCA effects was highly significant (r^2 = 0.99**). Va35, with the highest negative GCA effects, could be considered as a good combiner for low sensitivity or insensitivity. On the other hand, CM104 and Tx601 with high positive GCA effects indicated high combining ability for photoperiod sensitivity. The mean heterosis percentage was -10.96% (Table 26). indicating that in general hybrids tend to be less sensitive to photoperiod than their mid-parents.

Estimates of SCA effects of photoperiod sensitivity expressed in DTI are shown in Table 27. SCA effects would indicate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of their parental lines. Oh43 x Tx601 showed the highest negative SCA effects. This would mean that this hybrid combination made the best use of non-additive genes in contributing to low sensitivity to photoperiod. The reverse occurred in the case of high positive SCA effects, as in Va35 x Tx601. Generally, most hybrids showed negative SCA effect except Va35 x Oh43, B37 x Oh43 and Va35 x Tx601.

Table 27. Estimates of SCA effects of photoperiod sensitivity expressed in days to tassel initiation in a 5-entry diallel cross

	B37	Oh43	CM104	Tx601
Va35	-1.36	0.30	-0.32	3.63
B37		1.06	-1.22	-1.27
Oh43			-0.22	-3.27
CM104				-3.20

S.E. $(s_{ij} - s_{ik})$ = 1.94 S.E. $(s_{ij} - s_{kl})$ = 1.77

Leaf number data were also collected with the same set of 5 x 5 diallel cross. Since leaf number was highly correlated with days to tassel initiation, the difference in leaf number under the two daylength regimes would also reflect photoperiod sensitivity. Va35 again showed the lowest leaf gain (Table 28), while the tropical inbreds showed the highest leaf gains. Crosses between insensitive inbreds also showed low leaf gains indicating their low sensitivity to photoperiod. The crosses between insensitive and sensitive inbreds again showed reduced sensitivity to photoperiod as compared to its sensitive parent. The high to low negative GCA effects of Va35, B37 and Oh43 indicated their different combining abilities for photoperiod sensitivity. Similarly, high positive GCA effects were found in CM104 and Tx601. The coefficient of linear determination between the parental means and the GCA effects was highly significant (r^2 = 0.99**). Mean heterosis percentage was again negative, -18.30%.

Estimates of SCA effects (Table 29) also showed that in general all

Table 28. Photoperiod sensitivity expressed in leaf number and its GCA effects in a 5-entry diallel cross

	Va35	B37	Oh43	CM104	Tx601	GCA effects
Va35	0.27	0.80	1.17	2.97	3.93	-1.80
B37		1.50	1.53	3.37	3.80	-1.36
Oh43			2.73	4.50	5.03	-0.61
CM104				6.67	7.00	1.31
Tx601					9.73	2.46

BLSD (0.05) = 0.61

S.E. $(g_i - g_j)$ = 0.22

Mean heterosis % =-18.30

Table 29. Estimates of SCA effects of photoperiod sensitivity expressed in leaf number in a 5-entry diallel cross

	B37	Oh43	CM104	Tx601
Va35	0.29	-0.08	-0.21	-0.40
B37		-0.16	-0.25	-0.97
Oh43			0.14	-0.48
CM104				-0.44

S.E. $(s_{ij} - s_{ik})$ = 0.55

S.E. $(s_{ij} - s_{kl})$ = 0.50

hybrid combinations were negative except Va35 x B37 and Oh43 x CM104. In this case, B37 x Tx601 showed the highest negative SCA effects while Va35 x B37 had the highest positive SCA effects.

Genetic variances and heritabilities were also computed for these characters, on the assumption of a random model (Table 30). In both these characters, additive variance was the major component controlling the genetic variation of photoperiod sensitivity. This was shown by the high narrow sense heritability estimate obtained, 83.38% in DTI, and 94.70% in leaf number. The broad sense heritability was only slightly higher in both cases.

The graphical analyses of Hayman and Jink's (Hayman, 1954b) were also conducted for the sensitivity differences of these two characters. Analyses of variance of Wr - Vr (Table 31) were carried out to test the validity of the hypothesis postulated by Hayman (1954b). In both characters, there were no significant differences in the Wr - Vr values indicating that the assumptions in the diallel cross analyses had been fulfilled. The regression coefficients were both significantly different from zero and non-significant from unity. This confirms the results of the analyses of variance of Wr - Vr. Thus, non-allelic interaction would not account for the genetic variation of photoperiod sensitivity expressed in these two characters.

The VrWr graph based on days to tassel initiation are presented in Figure 15. Genes controlling photoperiod sensitivity exhibited partial dominance since the regression line intersected the Wr axis above the origin (a = 15.2069). The position of the points indicated genetic diversity of the inbred lines used in the diallel cross. The correlation coefficient between the parental and (Wr + Vr) values was low and

Table 30. Estimates of genetic variances and heritabilities of photoperiod sensitivity expressed in DTI and leaf number

	DTI	Leaf number
V_A	27.83 ± 216.51	6.51 ± 10.95
V_D	3.34 ± 6.50	0.19 ± 0.03
V_E	2.20 ± 0.35	0.17 ± 0.00
nh^2	83.38	94.70
bh^2	93.40	97.47

Table 31. Analyses of variance of Wr - Vr

		Mean squares	
	df	DTI	Leaf no.
Replications	2	0.012	0.0198**
Arrays	4	0.373	0.0003
Error	8	0.517	0.0010

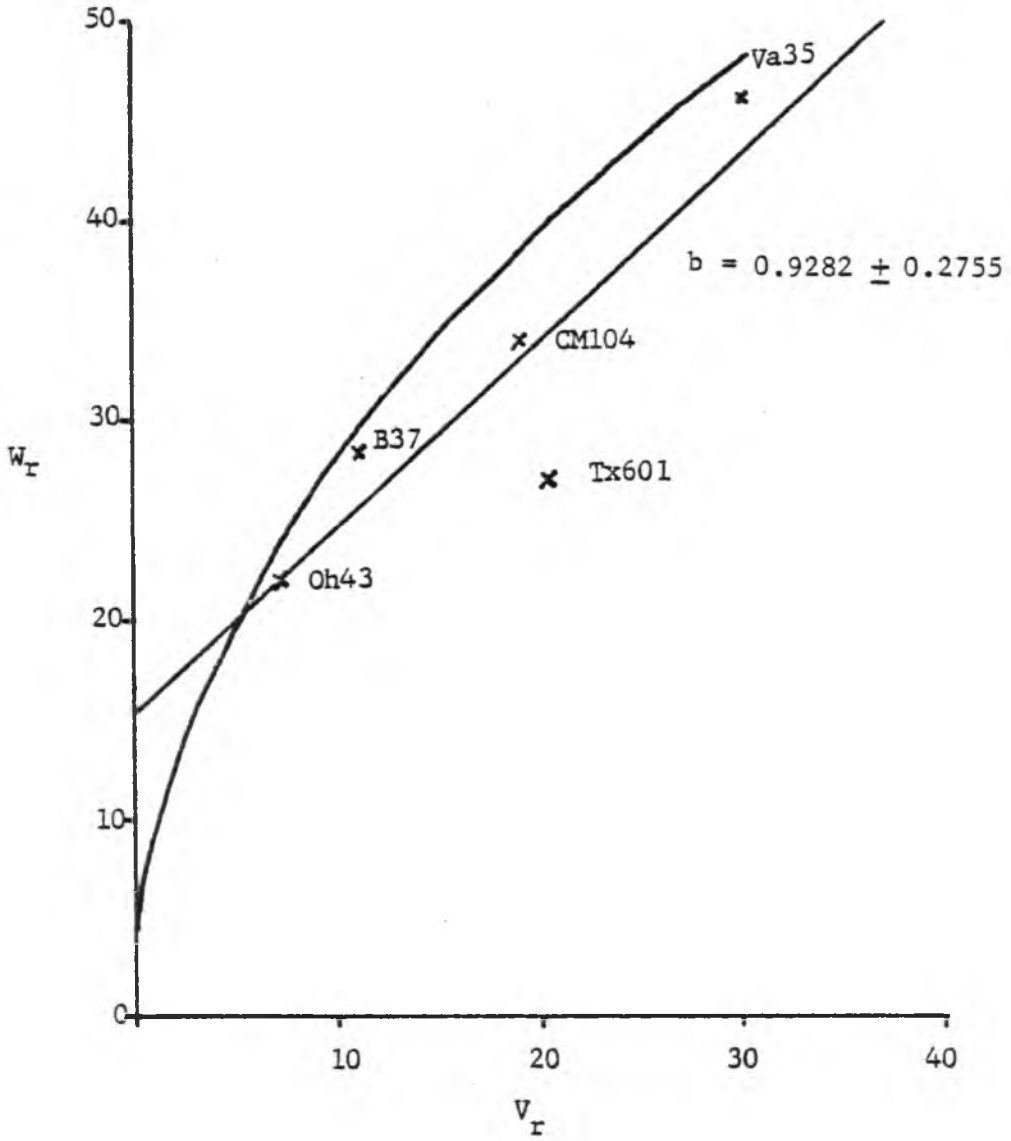

Figure 15. The regression of W_r on V_r for photoperiod sensitivity expressed in days to tassel initiation

negative (r = -0.22). This would mean that equal proportions of dominant genes influenced both high and low sensitivity to photoperiod, i.e. dominance was ambidirectional. The position of the parents on the regression line would have indicated the order of dominance if dominance was unidirectional. Nevertheless, the order of these parental lines in Figure 15 was Oh43, B37, Tx601, CM104 and Va35. The analysis of variance of the diallel table by Hayman and Jinks, as well as the components of variation were not presented here. However, estimates of heritability and gene numbers were extracted. Narrow and broad sense heritability using the formulas of Mather and Jinks (1971) were 81.9% and 93.0%, respectively. These high heritability estimates confirmed the results of the combining ability analyses. The k estimate in Hayman and Jinks diallel analysis would indicate the number of genes exhibiting some degree of dominance. In this case, the k value was 0.5 indicating that at least 1 gene controlling photoperiod sensitivity expressed in days to tassel initiation exhibited some degree of dominance.

The VrWr graph of photoperiod sensitivity expressed in leaf number is shown in Figure 16. The scatter of the points along the regression line indicated genetic diversity among the parental lines used in the diallel cross. The level of dominance was found to be partial dominance since the intercept cut the Wr axis above the origin (a = 3.5762). The correlation coefficient between the parental and (Wr + Vr) values in this case was significantly high and positive (r = 0.907). This suggested that low sensitivity to photoperiod was under the control of dominant genes. From the graph, it could be seen that the order of dominance was B37, Va35, Oh43, CM104 and Tx601. Thus, B37 would have

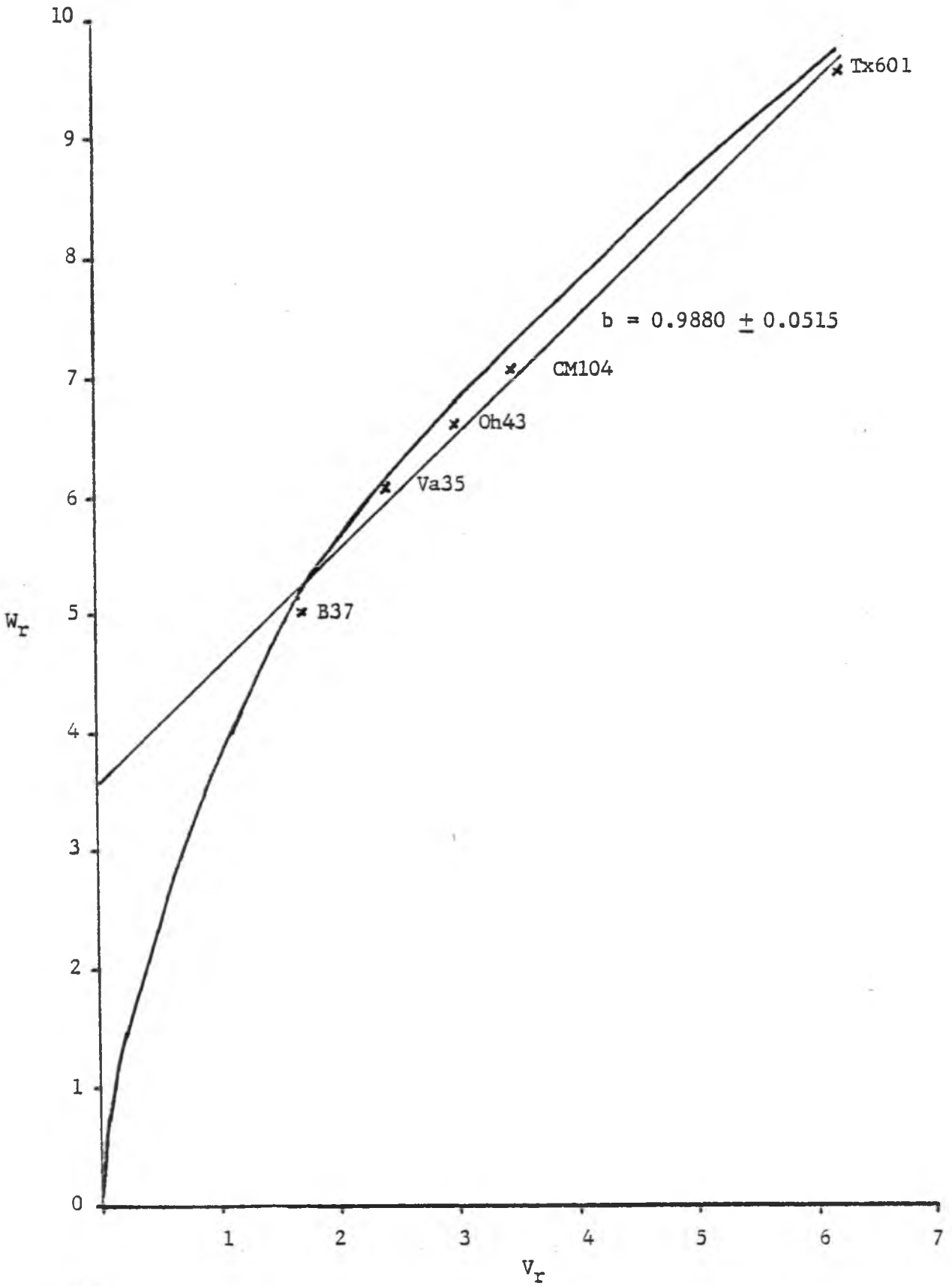

Figure 16. The regression of W_r on V_r for photoperiod sensitivity expressed in leaf number

the most number of dominant genes while Tx601 would have the most number of recessive genes. Narrow and broad sense heritability estimates using the formulas of Mather and Jinks (1971) were 94.9% and 97.3%, respectively. The k value in this case was 2.2 indicating that at least 2 genes controlling photoperiod sensitivity expressed in leaf number showed some degree of dominance.

The contrasting results of the graphical analyses for photoperiod sensitivity expressed in days to tassel initiation and leaf number may be attributed to the temporary waterlogging and phosphorus deficiency occurring in the field with the supplementary light. This may have affected tassel initiation time differentially thereby causing different results from photoperiod sensitivity expressed in leaf number. Although this may have delayed tassel initiation time slightly, it may not be serious enough to cause changes in leaf number.

6.2 10 x 10 Diallel Analysis

Ten inbreds of varying degrees of photoperiod sensitivity were chosen from the 43 inbreds originally screened in growth chambers to generate a diallel cross. Sensitivity expressed in days to anthesis and silking were the basis on which statistical analyses were carried out. Highly significant genotypic differences were found in these characters in all cases (Table 32). These data were then subjected to the diallel analysis of Griffing's Method 2 - Model 1.

The mean squares for GCA were highly significant in all cases (Table 33). SCA mean squares were also highly significant for both characters studied in Hawaii, and only significant at 5% for the characters studied in Illinois. This indicated that both additive and

Table 32. Analysis of variance of photoperiod sensitvity expressed in days to anthesis and silking in a 10-entry diallel cross

Source	df	Hawaii		df	Illinois	
		Days to anthesis	Days to silking		Days to anthesis	Days to silking
Replicate	2	91.69	129.40**	1	28.63**	2.25
Genotype	54	108.10**	108.91**	54	43.60**	58.32**
Error	108	4.54	6.28	54	3.67	3.81

Table 33. Mean squares for general and specific combining abilities and error of photoperiod sensitivity expressed in days to anthesis and silking

Characters	GCA	SCA	GCA/SCA	Error
Hawaii				
Days to anthesis	174.88**	8.27**	21.15	1.51
Days to silking	170.50**	9.46**	18.01	2.10
Illinois				
Days to anthesis	107.10**	4.74*	22.61	1.84
Days to silking	152.99**	4.39*	34.85	1.91

non-additive genetic variation did contribute to the control of photoperiod sensitivity in corn. However, the GCA/SCA ratio was many times greater than unity, suggesting that additive genetic variation was predominant.

The sensitivity difference due to photoperiod expressed in days to anthesis and silking evaluated in Hawaii was presented in Table 34. The 10 inbreds were arranged according to their parental means based on the sensitivity expressed in days to anthesis from low to high sensitivity. Va35 showed the lowest sensitivity to photoperiod, while Tx601 was the greatest. Referring to the results on the days to anthesis, the other inbreds which showed no significant difference from Va35 were Hi25, B37 and A619. Crosses among these inbreds also showed no significant difference from Va35 indicating that insensitive x insensitive crosses would produce insensitive genotypes. Oh43, Mo17 and Hi26 were significantly different from Va35. Their crosses with the other insensitive inbreds produced mainly insensitive genotypes which did not differ significantly from Va35, although exceptions did occur. Crosses among inbreds of intermediate sensitivity also produced similar photoperiod reactions. Oh43 which was supposed to be insensitive did not perform as such, and this might be due to the temporary waterlogging and phosphorus deficiency problems mentioned earlier.

Among the tropical inbreds, Hi30 could be considered as less sensitive to CM104 and Tx601. Crosses among themselves or with the insensitive inbreds produced genotypes which showed reduced sensitivity to photoperiod although majority of these were still sensitive. The mean heterosis percentage was negative indicating that hybrids in

Table 34. Photoperiod sensitivity expressed in days to anthesis and silking and their GCA effects in a 10-entry diallel cross in Hawaii

	Va35	Hi25	B37	A619	Oh43	Mo17	Hi26	Hi30	CM104	Tx601	GCA effects
Va35	9.3[a]	9.7	12.3	11.2	12.2	10.8	14.8	15.6	16.0	21.8	-2.72
	11.7	12.0	15.2	15.1	15.1	13.1	17.2	19.3	18.2	25.5	-2.52
Hi25		11.7	11.1	11.8	11.4	12.0	13.4	17.5	16.6	21.9	-2.26
		14.3	12.7	13.9	15.5	14.3	14.2	21.0	17.6	23.5	-2.58
B37			11.8	11.0	11.8	10.2	11.9	15.4	19.9	17.7	-2.58
			13.0	13.8	14.2	12.8	14.7	18.0	23.2	19.0	-2.90
A619				12.4	13.2	9.9	12.6	16.2	19.1	17.4	-2.39
				17.7	18.0	11.8	15.0	19.7	22.7	19.4	-1.61
Oh43					14.5	11.2	13.9	15.4	19.6	19.9	-1.52
					17.3	13.0	16.2	18.0	22.0	21.4	-1.35
Mo17						14.6	13.7	15.1	19.4	19.8	-2.04
						18.4	14.2	18.0	23.2	21.5	-2.13
Hi26							16.4	13.7	17.8	17.7	-1.13
							18.1	15.1	19.6	18.6	-1.94
Hi30								18.8	17.1	25.1	1.07
								23.3	20.3	29.9	1.82
CM104									32.5	26.8	5.13
									35.4	30.9	5.35
Tx601										44.5	8.43
										44.4	7.86

[a]Upper and lower values represent days to anthesis and silking respectively

BLSD (0.05) = 3.1 / 3.6 S.E. ($g_i - g_j$) = 0.50 / 0.59 Mean heterosis % = -12.85 / -13.30

general had the inclination towards low photoperiod sensitivity.

Sensitivity to photoperiod expressed in days to silking (Table 34) on the same set of 10 entry diallel cross also showed similar trends to the data expressed in days to anthesis. The mean heterotic effect was again negative.

The GCA effects for photoperiod sensitivity expressed in both characters (Table 34) indicate that temperate inbreds had high negative GCA effects. This suggested that they were good combiners for low sensitivity to photoperiod especially Va35, Hi25, B37, A619 and Mo17. On the other hand, CM104 and Tx601 showed high positive GCA effects suggesting that both these inbreds were good combiners for high sensitivity.

Estimates of SCA effects for photoperiod sensitivity expressed in both anthesis and silking are presented in Appendix 5. The following hybrid combinations, B37 x Tx601, A619 x Tx601, Hi26 x Tx601 and Hi30 x CM104 showed high negative SCA effects for photoperiod sensitivity expressed in both characters. This indicates that they made the best use of non-additive genes for low sensitivity to photoperiod.

The same set of diallel cross was evaluated under the long summer days at the University of Illinois. Sensitivity expressed in days to anthesis and silking (Table 35) were computed using the mean values in Hawaii as controls. Referring to the data on the photoperiod sensitivity expressed in days to anthesis, Va35 again showed the lowest sensitivity to photoperiod. Hi25, B37, A619 and Mo17 showed no significant difference from Va35. The tropical inbreds again showed large sensitivity differences. However, in this planting, Tx601 showed lesser sensitivity as compared to CM104. Tx601 as well as the hybrid

Table 35. Photoperiod sensitivity expressed in days to anthesis and silking and their GCA effects in a 10-entry diallel cross evaluated in Illionis

	Va35	Hi25	B37	A619	Oh43	Mo17	Hi26	Hi30	CM104	Tx601	GCA effects
Va35	9.7[a]	7.8	8.2	9.1	10.1	9.9	13.6	12.2	14.0	16.9	-2.48
	9.2	7.9	9.1	9.6	11.8	10.9	15.0	14.1	14.6	17.8	-3.36
Hi25		12.5	10.9	10.4	11.1	11.4	13.8	15.1	17.4	12.3	-1.32
		14.9	11.8	10.9	12.0	12.2	15.2	17.3	20.6	13.7	-1.51
B37			10.3	7.9	10.6	11.2	10.6	11.9	18.1	10.8	-2.52
			8.7	9.2	10.8	10.8	12.7	15.0	19.4	11.5	-3.48
A619				8.9	11.5	5.5	10.9	14.2	16.2	16.0	-2.62
				9.5	13.0	7.3	12.4	17.7	20.0	16.3	-2.84
Oh43					15.0	12.2	13.5	13.0	19.8	15.6	-0.30
					17.0	9.2	15.3	17.3	24.5	18.3	-0.27
Mo17						8.5	11.8	13.7	17.7	15.0	-2.13
						10.3	13.0	18.2	20.8	17.1	-2.45
Hi26							15.2	15.3	18.3	14.4	0.13
							15.4	19.6	20.5	15.8	0.07
Hi30								17.5	25.5	20.8	2.14
								23.0	27.2	25.2	4.01
CM104									33.2	17.0	6.62
									34.1	20.1	7.20
Tx601										21.0	2.48
										22.7	2.64

[a] Upper and lower values represent days to anthesis and silking respectively

BLSD (0.05) = 3.4 S.E. ($g_i - g_j$) = 0.55 Mean heterosis % = -10.04
3.5 0.56 - 6.44

CM104 x Tx601 showed differences in sensitivity when compared to the photoperiod sensitivity data from Hawaii. On the whole, the results from Illinois were slightly lower in sensitivity difference as compared to Hawaii. Nevertheless, the trend in both locations was similar, with some exceptions.

Photoperiod sensitivity expressed in days to silking in the Illinois planting (Table 35) corresponded well in general with that expressed in days to anthesis. With some exceptions, the trend obtained in Illinois was also similar to that in Hawaii. There was a high and significant correlation between data of both locations for photoperiod sensitivity expressed in days to anthesis ($r = 0.74^{**}$) and silking ($r = 0.75^{**}$). In both characters, a negative mean heterosis percentage was obtained.

GCA effects obtained (Table 35) showed negative effects for temperates and positive effects for tropical inbreds with the exception of Hi26. This again reflected the different degrees of photoperiod sensitivity in this 10 entry diallel cross.

Estimates of SCA effects of photoperiod sensitivity for both characters are presented in Appendix 6. High negative SCA effects for photoperiod sensitivity expressed in days to anthesis were obtained for the following crosses, A619 x Mo17, Va35 x CM104 and CM104 x Tx601. In the case of photoperiod sensitivity expressed in days to silking, high negative SCA effects were obtained for Oh43 x Mo17, Va35 x CM104 and CM104 x Tx601.

Genetic variances and heritability estimates were also calculated on the assumption of a random model. These are shown in Tables 36 and 37 for Hawaii and Illinois locations, respectively. In all cases,

Table 36. Estimates of genetic variances and heritabilities of photoperiod sensitivity expressed in days to anthesis and silking from the 10-entry diallel

	Days to anthesis	Days to silking
V_A	27.77 ± 94.44	26.84 ± 89.78
V_D	6.75 ± 3.08	7.37 ± 4.06
V_E	1.51 ± 0.04	2.10 ± 0.08
nh^2	77.06	73.93
bh^2	95.80	94.23

Table 37. Estimates of genetic variances and heritabilities of photoperiod sensitivity expressed in days to anthesis and silking from the 10 entry diallel evaluated in Illinois

	Days to anthesis	Days to silking
V_A	17.06 ± 35.42	24.77 ± 72.25
V_D	2.90 ± 1.12	2.49 ± 0.99
V_E	1.84 ± 0.12	1.19 ± 0.14
nh^2	78.28	84.94
bh^2	91.58	93.46

the additive variance was comparatively larger than the dominance variance, as well as the environmental variance. This therefore resulted in high narrow sense as well as broad sense heritability estimates for photoperiod sensitivity expressed in both days to anthesis and silking.

6.3 Generation Mean Analysis

Crosses involving photoperiod insensitive and sensitive inbreds and their advanced populations were evaluated under extended daylength in Hawaii and under the long summer days to Illinois and Nebraska. The average days to anthesis for the six population means, that is, P_1, P_2, F_1, F_2, B_1 and B_2 of these crosses are presented in Table 38. In general, the two parental lines, P_1 and P_2 exhibited big differences in terms of days to anthesis, except for crosses involving Hi30. The cross B73 x Hi30 evaluated in Nebraska showed unexpected results whereby Hi30, a photoperiod sensitive inbred flowered earlier than the photoperiod insensitive inbred B73. No explanations could be offered in view of the fact that Hi30 flowered much later in Illinois. Although data for this cross is presented, it is not included in the interpretation.

In comparing the F_1 population mean with the parental means for all the crosses, it was found that in general the F_1 means were intermediate between the two parental means and exhibiting partial dominance towards low sensitivity. This confirmed the results of the diallel crosses. Exceptions were obtained in a few crosses, i.e. B73 x CM104 and B73 x Tx601 in Hawaii, Va35 x Hi30 in Nebraska, and B73 x Hi30 and B73 x Tx601 in Nebraska. The F_1 means did not differ

Table 38. Average days to anthesis of the parents and crosses under long days

Crosses	P1	P2	F1	F2	B1	B2	A	B	C
Hawaii									
Va35 x CM104	64.6	92.2	77.0	78.9	71.5	84.5	- 1.4	- 0.2	4.8
B37 x CM104	70.8	92.2	79.8	81.0	75.6	77.8	0.6	-16.4**	1.4
B37 x Tx601	70.8	94.3	76.2	83.6	76.9	88.3	6.8	6.1	16.9*
Oh43 x CM104	70.0	92.2	79.1	77.9	70.6	83.0	- 7.9**	- 5.3	- 8.8
B73 x CM104	78.8	92.2	78.6	82.8	75.9	80.9	- 5.6	- 9.0	3.0
B73 x Tx601	78.8	94.3	72.4	76.9	73.4	81.6	- 4.4	- 3.5	-10.3*
Illinois									
Va35 x Hi30	70.8	79.5	70.8	82.8	75.3	77.9	9.0	5.5	39.3**
Va35 x Tx601	70.8	98.0	82.5	89.1	83.2	89.7	-14.1**	- 1.1	22.6**
Oh43 x Hi30	74.3	79.5	74.9	72.4	71.5	76.4	- 6.2	- 1.6	-14.0*
Oh43 x Tx601	74.3	98.0	77.4	89.0	80.6	91.9	9.5*	8.4	28.9**
Nebraska									
Va35 x Tx601	59.0	92.6	65.9	68.0	62.4	73.0	- 0.1	-12.5*	-11.4
B73 x Hi30	67.8	66.6	61.8	61.9	59.6	61.4	-10.4**	- 5.6	-10.4*
B73 x Tx601	67.8	92.6	67.2	71.2	67.9	76.5	0.8	- 6.8	-10.0

greatly from the F_2 means with the exception of B37 x Tx601 in Hawaii, and Va35 x Hi30, Va35 x Tx601 and Oh43 x Tx601 in Illinois. In all cases the backcross means showed shifts towards their respective recurrent parents in majority of the cases.

Frequency distributions of these crosses involving insensitive and sensitive inbreds are presented in Figures 17, 18, 19 and 20. Within each location, the data from the common parental lines were pooled together. In all cases frequency distributions of the parental populations were well separated from each other except with Hi30, which was only moderately sensitive to photoperiod. The F_1 distribution in general was situated intermediate between their respective parental distributions.

The F_2 showed a bimodal distribution in a few cases, notably Oh43 x CM104 and Va35 x CM104 (Hawaii, Figure 17), B37 x Tx601 (Hawaii, Figure 18) and Va35 x Hi30 (Illinois, Figure 19). However, in all cases the F_2 was widely distributed, thereby suggesting the possible segregation of major genes for photoperiod sensitivity. The backcrosses again showed distinct skewness towards the parents except for the backcross distributions of B37 x CM104 (Hawaii, Figure 18), Va35 x Hi30 (Illinois, Figure 19). The backcross distributions were generally widely dispersed, and all the B_2 distributions clearly indicate that selection for low photoperiod sensitivity (or early segregants) is possible. There is no clear cut evidence of transgressive segregation in the segregating populations studied.

It must be pointed out that the results from the generation mean analyses would not only reveal the inheritance of photoperiod sensitivity but also included an intrinsic portion attributed to maturity. These

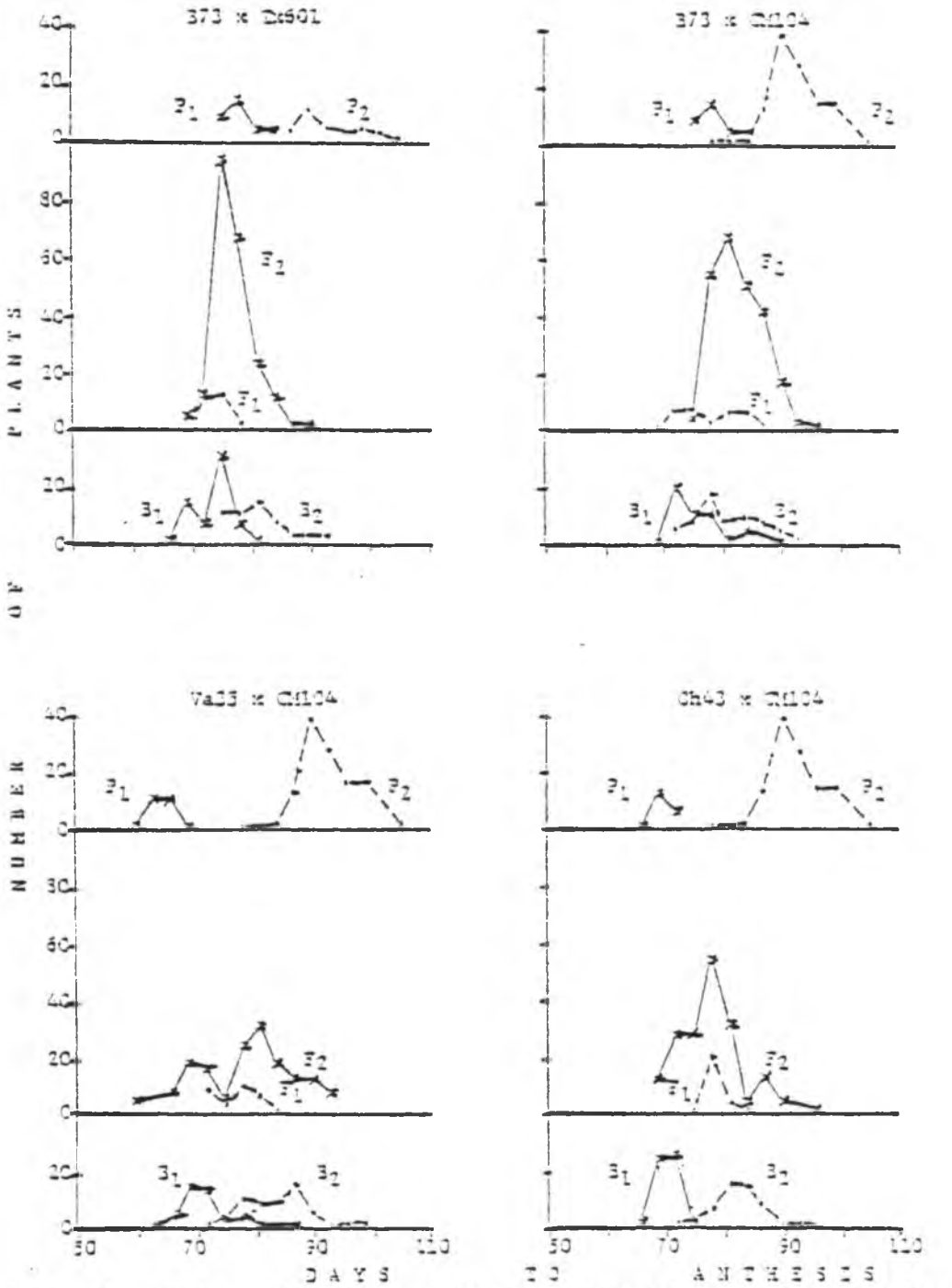

Figure 17. Frequency distributions of days to anthesis in genetic populations planted under extended daylength in Hawaii

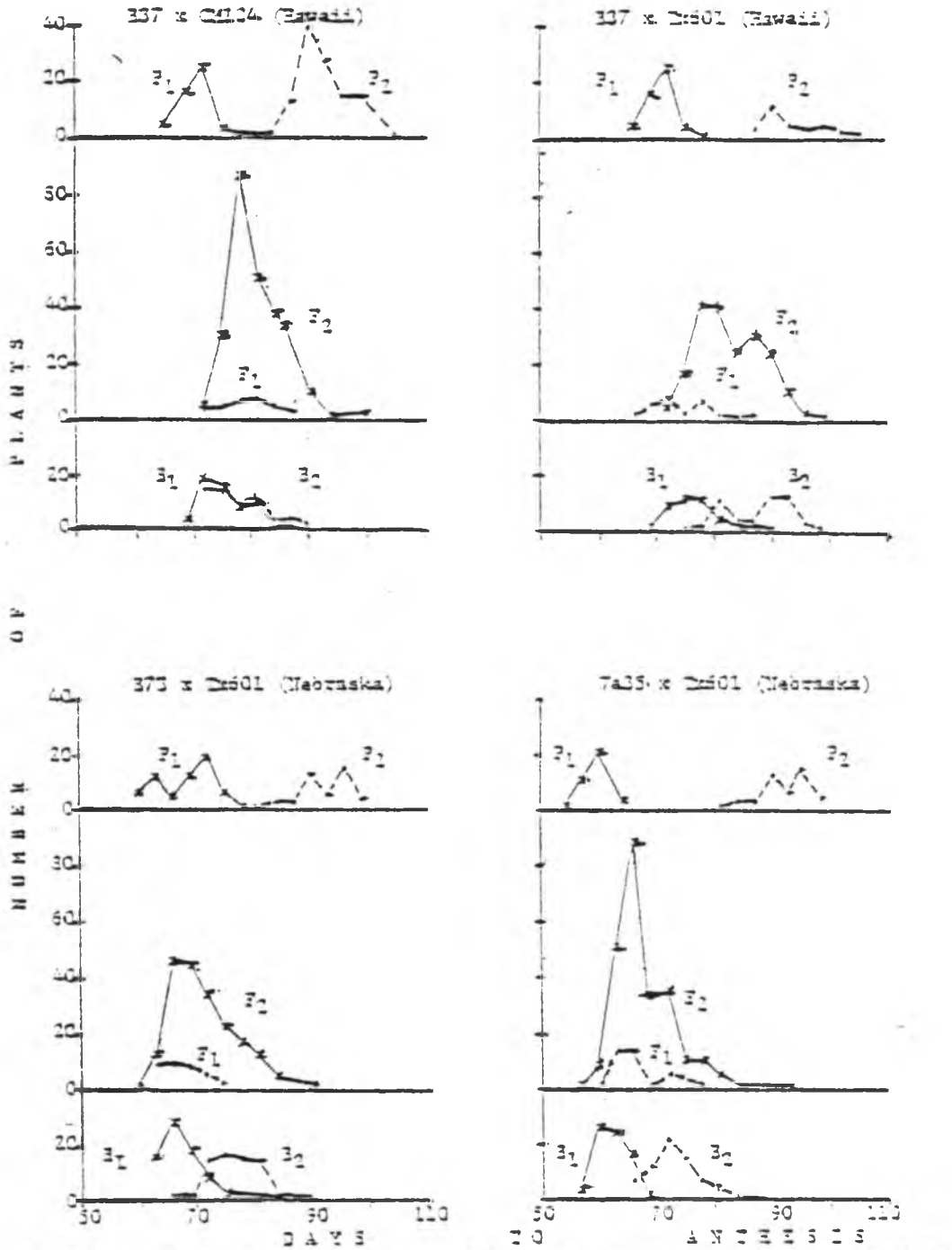

Figure 13. Frequency distributions of days to anthesis in genetic populations planted in Hawaii and Nebraska.

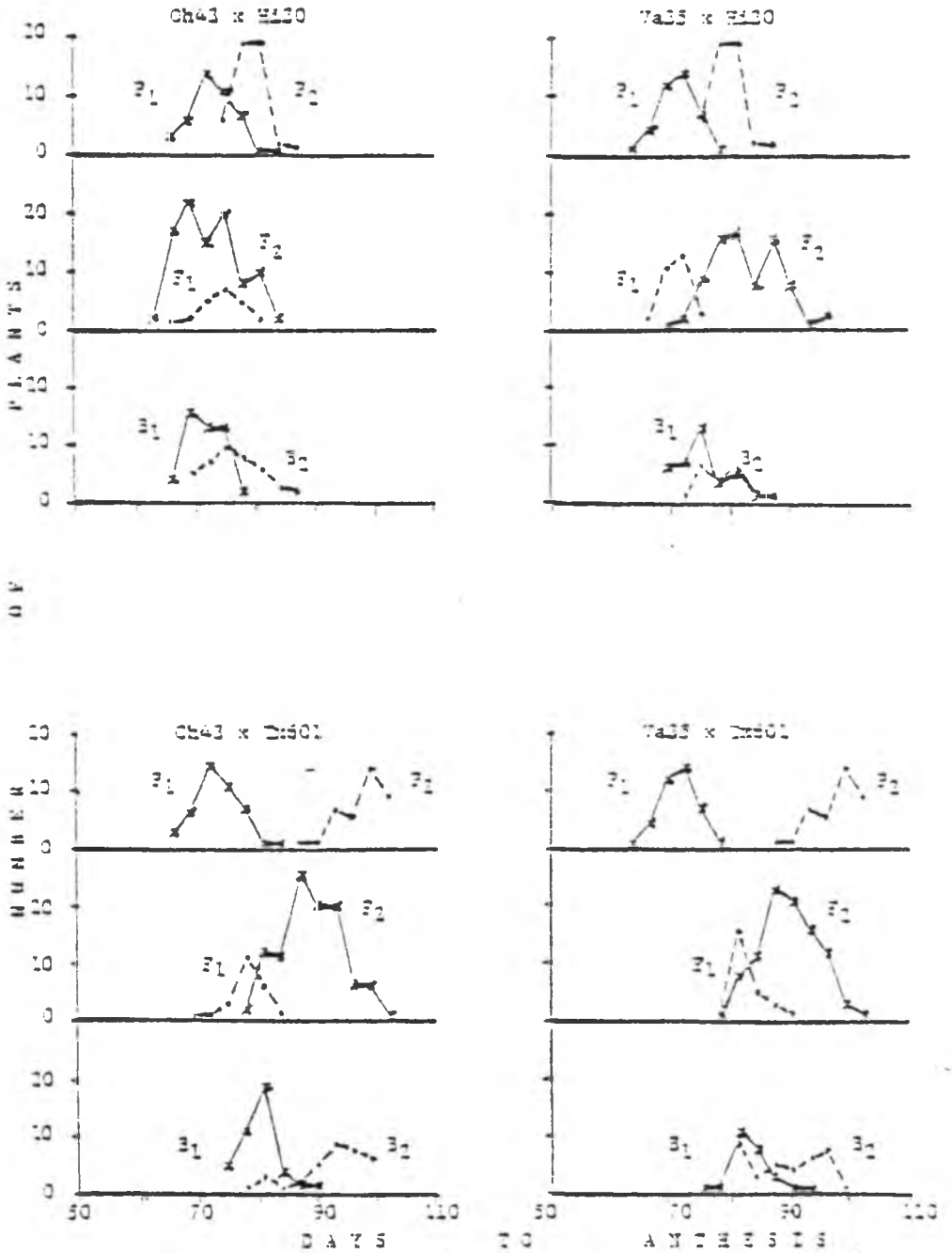

Figure 19. Frequency distributions of days to anthesis in genetic populations planted in Illinois

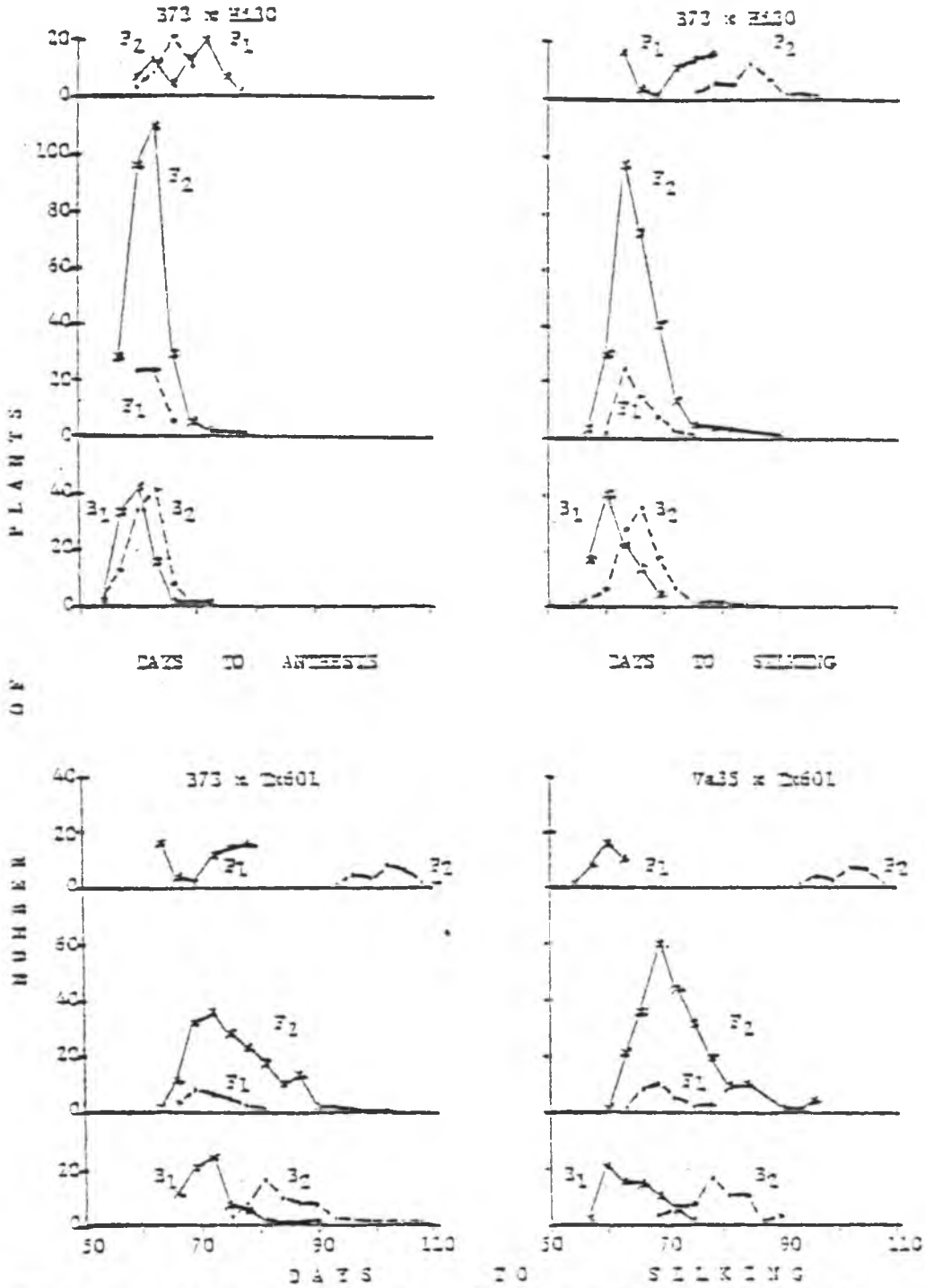

Figure 20. Frequency distributions of days to anthesis and silking in genetic populations planted in Nebraska

two attributes or traits were so closely confounded in controlling flowering that there was no possibility of separating the two effects in this study. Possible alternatives in future experiments would be discussed later. As a result of such interaction, genetic interpretations regarding photoperiod sensitivity must be approached with caution in the generation mean analyses. From here onwards, genetic interpretations would be referred to the character evaluated per se, that is, days to anthesis, but with a reminder that photoperiod sensitivity was also involved since all the populations were evaluated under long day conditions. Table 39 would clearly indicate that the P_1 and P_2 lines in the generation mean crosses also involved different maturity classes with the exception of Hi30 which was an early photoperiod sensitive inbred.

Scaling tests as outlined by Mather and Jinks (1971) were used to assess the adequacy of the additive-dominance model for all the crosses (Table 38). The quantities A, B and C did not differ significantly from zero within the limits of sampling error only for the crosses Va35 x CM104 (Hawaii), B73 x CM104 (Hawaii) and B73 x Tx601 (Nebraska). This would indicate that epistasis was absent in these crosses. However, in the other crosses, significant differences were obtained in one or two of the A, B and C values suggesting the presence of epistasis or non-allelic interaction in days to anthesis under long day conditions.

In the absence of epistasis as suggested by the scaling tests, a three-parameter model as described by Mather and Jinks (1971) was applied to the six population means of the three crosses (Table 40). This included a mean (m) which was the mid-parental value in the absence of epistasis, an additive genetic component (a), and a dominance

Table 39. Average days to anthesis and growing degree days (GDD) of the parental lines grown under normal short day conditions on March 15, 1977 in Hawaii

Temperate inbreds	Days to anthesis	GDD	Tropical inbreds	Days to anthesis	GDD
B37	59.5	1383	CM104	64.3	1500
B73	60.0	1395	Hi30	58.4	1356
Oh43	56.2	1303	Tx601	71.9	1685
Va35	57.6	1337			

Table 40. Estimates of the components of generation means for days to anthesis fitting a three-parameter model and their joint scaling tests

	Hawaii		Nebraska
	Va35 x CM104	B73 x CM104	B73 x Tx601
m	78.53**	85.33**	79.51**
a	-13.72**	- 6.58**	-11.60**
d	- 0.86	- 7.11**	-14.24**
X^2	0.34	6.55	2.66
P	0.98 - 0.95	0.10 - 0.05	0.50 - 0.30

genetic component (d). The X^2 values were lower than the critical X^2 value for P = 0.05, i.e. non-significant. This joint scaling test again confirmed the A, B, C scaling tests of Table 38, that epistasis was not important in the inheritance of days to anthesis for these three crosses. Highly significant additive genetic effect was detected for all the three crosses. Similarly, high dominance genetic effect was also detected except for the cross Va35 x CM104 (Hawaii). With the exception of this cross, both additive and dominance gene actions were important in controlling days to anthesis, with earlier anthesis being dominant as indicated by the negative sign.

The six parameter model as outlined by Hayman (1958, 1960) and using the notations of Gamble (1962) was applied to all crosses including the above three (Table 41). The six gene effects obtained were the F_2 mean (m), the additive gene effect (a), the dominance gene effect (d), the additive x additive epistatic effect (aa), the additive x dominance epistatic effect (ad) and the dominance x dominance epistatic effect (dd). According to Mather and Jinks (1971), finding the epistatic effects, aa, ad, or dd significant was equivalent to finding a significant deviation from zero in the scaling tests. However, only two of the crosses, i.e. Va35 x CM104 (Hawaii) and B73 x x Tx601 (Nebraska) confirmed the absence of epistasis as tested by the individual and joint scaling tests. The cross B73 x CM104 (Hawaii) was found to have significant aa and dd epistatic effects even though epistasis was found to be absent in the previous test. These results indicate that if a particular cross fitted a 3 parameter model, estimation of gene effects on a 6 parameter model would cause unreliable estimates of gene effects.

Table 41. Mean estimates of the six gene effects for days to anthesis under long days

Crosses	m	a	d	aa	ad	dd
Hawaii						
#Va35 x CM104	78.91**	-13.04**	- 5.00	- 3.64	-0.76	2.42
B37 x CM104	81.01**	- 2.25	-18.90*	-17.30*	8.45**	34.52*
B37 x Tx601	83.64**	-11.45**	-10.35	- 4.14	0.30	- 8.81
Oh43 x CM104	77.87**	-12.38**	- 6.40	- 4.40	-1.28	17.62
#B73 x CM104	82.84**	- 5.06	-24.50**	-17.80*	1.64	32.18*
B73 x Tx601	76.88**	- 8.20**	-11.75*	2.40	-0.45	5.52
Illinois						
Va35 x Hi30	82.76**	- 2.63	-29.15**	-24.80**	1.72	10.24
Va35 x Tx601	89.14**	- 6.51*	-12.50	-10.60	7.09*	- 1.46
Oh43 x Hi30	72.36**	- 4.85	4.20	6.20	-2.25	1.55
Oh43 x Tx601	88.99**	-11.26**	-19.75*	-11.00	0.59	- 6.95
Nebraska						
Va35 x Tx601	68.01**	-10.62**	-11.10	1.20	6.18*	13.72
B73 x Hi30	61.90**	- 1.80	-11.00*	- 5.68	-2.40	21.64*
#B73 x Tx601	71.23**	- 8.68**	- 9.00	3.88	3.72	1.98

Fitted on a 3-parameter model

In the remaining crosses (Table 41), fitting a six parameter model did not detect significant epistatic gene effects for the following crosses, B37 x Tx601 (Hawaii), Oh43 x CM104 (Hawaii), B73 x Tx601 (Hawaii), Oh43 x Hi30 (Illinois) and Oh43 x Tx601 (Illinois). Out of these 5 crosses, Oh43 x Hi30 (Illinois) did not have significant a or d genetic effects. This might have been due to the close proximity of the two parental values in days to anthesis, and thereby resulting in the failure of detection significant gene effects. Highly significant additive gene action was found in the other 4 crosses. Although the dominance gene effects were proportionately large in these 4 cases, significance was obtained only for B73 x Tx601 (Hawaii), Oh43 x Tx601 (Illinois).

Significant epistatic gene effects were obtained for B37 x CM104 (Hawaii), Va35 x Hi30 (Illinois), Va35 x Tx601 (Illinois), Va35 x Tx601 (Nebraska) and B73 x Hi30 (Nebraska). Except for B37 x CM104 (Hawaii) which showed significant differences for all three epistatic gene effects, the others showed significant difference only in one of the three epistatic gene effects.

It must be pointed out that the sign of the parameters a and ad was dependent on the parents which were considered as P_1 or P_2. Thus the sign for these two parameters was meaningless and could be ignored. In general it could be concluded that days to anthesis under long days were under the control of additive genetic effect as well as dominance genetic effect, depending on the crosses. Epistasis was found to influence the inheritance of this trait only in some cases. Earlier flowering was found to be dominant to late flowering as indicated by the negative signs in almost all the d parameter.

The same set of crosses evaluated under different locations and environments had almost similar results. The crosses were B73 x Tx601 evaluated under extended daylength in Hawaii and under the natural long days of Nebraska, and also Va35 x Tx601 evaluated in Illinois and Nebraska.

Components of genetic variation (Table 42) were estimated on the assumption of no epistasis and linkage. In general, the additive variance was much larger than the dominance and environmental variance. However, the environmental variance was still considerably large, and this resulted from the big variance of the non-segregating populations, i.e. P_1, P_2 and F_1. The parental lines are inbreds which are of low vigor and easily succumb to environmental fluctuations. In addition, genotypes with delayed flowering as a result of photoperiod sensitivity tend to have a larger period of opportunity for disease and insect infestations. This will cause the large variation encountered. As a result of this as well as the small variance associated with the F_2 populations in some cases, there was a preponderance of negative dominance variance in this study.

Narrow sense heritability estimates (Table 42) following the formula of Warner (1952) were obtained for all crosses. This was high for a number of crosses, especially crosses involving Va35. With the exception of the cross Oh43 x Tx601 (Illinois), crosses involving Oh43 also had high narrow sense heritability estimate. The values of narrow sense heritability varied widely and on the average, the estimate was 57.43% for days to anthesis under long days which was considerably high.

Table 42. Genetic variances and heritability estimates for days to anthesis under long days

Crosses	V_A	V_D	V_E	nh^2	bh^2
Hawaii					
Va35 x CM104	58.53	-15.27	10.46	108.96	80.46
B37 x CM104	13.94	- 2.77	11.41	61.76	49.47
B37 x Tx601	6.06	11.03	10.03	22.35	68.02
Oh43 x CM104	32.52	-11.76	6.96	117.34	74.89
B73 x CM104	- 5.15	12.67	7.65	- 33.95	49.57
B73 x Tx601	4.70	- 2.03	8.40	42.51	24.12
Illinois					
Va35 x Hi30	38.67	- 7.26	6.32	102.87	83.25
Va35 x Tx601	12.23	3.39	6.37	55.61	71.03
Oh43 x Hi30	14.27	0.68	7.79	62.77	65.74
Oh43 x Tx601	6.53	10.97	8.36	25.24	67.67
Nebraska					
Va35 x Tx601	22.25	- 9.43	11.06	93.20	53.68
B73 x Hi30	3.28	- 3.88	9.09	38.69	- 7.03
B73 x Tx601	26.00	-10.54	14.32	49.24	51.92
Average	17.99	- 1.86	9.09	57.43	55.98

Broad sense heritability estimates were also computed by the conventional method using the three non-segregating populations to estimate environmental variance. These estimates were lower than the narrow sense heritability in most cases because of the high frequency of negative dominance variance. As a result the average estimate was also smaller, which was 55.98%.

Estimates of minimum number of genes were made following the Castle-Wright formula (Mock and Schuetz, 1974), and another formula attributed to Sewall Wright (Mock and Schuetz, 1974). There was no clear cut consistency in the gene number estimates as shown in Table 43. This ranged from as low as 1 to as high as about 13 genes conditioning days to anthesis. However, on the average, it was found that 4 to 5 genes controlled days to anthesis under long days in this study. These few genes could be attributed to be responsible for maturity, i.e. days to anthesis, as well as photoperiod sensitivity. However, it must be noted that the estimates of minimum gene number could be biased downward by epistasis and non-additivity of genes.

One possibility of obtaining genetic interpretation of photoperiod sensitivity in the generation mean analysis was by studying crosses of insensitive x sensitive inbreds, whereby the parental lines were of comparable maturity. This might be possible for the crosses Va35 x Hi30 and Oh43 x Hi30, both evaluated in Illinois (Table 43). B73 x Hi30 (Nebraska) would not be considered as described earlier. The narrow sense heritability estimate for these two crosses were 102.87% and 62.77% respectively, with an average of 82.82%. This high narrow sense heritability for photoperiod sensitivity supported the results

Table 43. Estimates of minimum number of genetic factors controlling days to anthesis

Crosses	Castle-Wright	Sewall Wright
Hawaii		
Va35 x CM104	2.29	2.30
B37 x CM104	9.72	9.84
B37 x Tx601	4.22	4.83
Oh43 x CM104	2.47	2.51
B73 x CM104	1.94	2.97
B73 x Tx601	4.83	12.88
Illinois		
Va35 x Hi30	0.29	0.44
Va35 x Tx601	6.04	6.09
Oh43 x Hi30	0.22	0.28
Oh43 x Tx601	4.41	5.61
Nebraska		
Va35 x Tx601	10.78	12.66
B73 x Hi30	0.03	1.44
B73 x Tx601	4.87	7.54
Average	4.01	5.34

obtained from the diallel cross analyses. Minimum gene number estimates were low in both cases, and could be attributed to a minimum of 1 gene. This also confirmed the minimum number of effective factors obtained by Hayman and Jinks' diallel cross analysis, which was 1 to 2 genes exhibiting some degree of dominance. Thus photoperiod sensitivity could be under the control of a minimum of 1 to 2 genes.

Days to silking was also collected for the crosses at the University of Nebraska. The six population means of the three crosses are shown in Table 44. The P_1 and P_2 means were widely dispersed except for the cross B73 x Hi30. The F_1 and F_2 means did not differ greatly in all cases. The backcross means showed a strong shift towards the recurrent parent except for the cross B73 x Hi30. Frequency distribution of the six populations (Figure 20) also supported the above results. The F_2 distribution of B73 x Tx601 was bimodal. Nevertheless both F_2 distributions for the two crosses, B73 x Tx601 and Va35 x Tx601 were widely dispersed suggesting a possible segregation of major genes for days to silking under long days. The B_2 distributions (i.e. backcross to the sensitive parent) for both crosses were also broadly dispersed indicating that selection for early (or photoperiod insensitive) segregants was possible.

These data were not subjected to the usual scaling tests as well as estimation of gene effects. However, components of genetic variation were estimated (Table 45). Results obtained were similar to that on days to anthesis. In general, the additive variance was larger than the dominance and environmental variation. However, the environmental variance estimated from the nonsegregating populations were again very large resulting in a negative estimate for dominance variation.

Table 44. Average days to silking of the parents and crosses planted in Nebraska

Crosses	P_1	P_2	F_1	F_2	B_1	B_2
Va35 x Tx601	59.9	102.0	69.7	72.2	64.6	79.0
B73 x Hi30	70.7	75.1	65.4	65.4	61.7	66.2
B73 x Tx601	70.7	102.0	71.5	76.0	72.1	84.8

Table 45. Genetic variances, heritability and minimum gene number estimates for days to silking planted in Nebraska

Crosses	V_A	V_D	V_E	nh^2	bh^2	Genetic factors	
						Castle-Wright	Sewal Wright
Va35 x Tx601	40.32	-10.04	9.56	101.21	76.00	7.28	8.31
B73 x Hi30	9.09	- 4.22	15.48	44.67	23.90	0.22	1.50
B73 x Tx601	25.01	6.80	14.64	53.84	68.49	4.08	5.91
Average	24.81	- 2.49	13.23	66.57	56.13	3.86	5.24

Narrow sense heritability following the formula of Warner (1952) was obtained and ranged from 44.67% to 101.21% with an average of 66.57%. Broad sense heritability calculated in the conventional method was lower due to the negative dominance variance and averaged 56.13%.

The minimum gene number was also estimated for days to silking under long day evaluation and was found to range widely. The average gene number for days to silking was 4 to 5 genes using the two different formulas. This was the same as the result obtained for days to anthesis.

6.4 Discussion

There has been some recent interest in the use of exotic germplasm by corn breeders to broaden genetic variability (Lonnquist, 1974; Brown, 1975) especially after the 1970 Southern Corn leaf blight epiphytotics in the Corn Belt. Use of exotic germplasm, however, is a problem since they are late maturing due to its sensitivity to photoperiod (Brown and Goodman, 1977). These photoperiod sensitive genotypes must therefore be converted to low photoperiod sensitivity for effective and widespread use. Knowledge of the inheritance of photoperiod sensitivity will therefore be of great importance in indicating the breeding methods to be used and the feasibility of achieving low sensitivity to photoperiod through breeding.

Correct genetic interpretations of any trait will depend largely on the proper separation of effects. Murfet (1977) stated that a genetic study of the flowering process requires, among other things, an adequate separation of effects on the initiation and development phases, use of controlled, as well as field environments to separate temperature

and photoperiod effects. In the genetic study using the diallel cross, effects such as temperature as well as maturity were separated out, ignoring the negligible effect of the low light intensity of the incandescent lamps. This was achieved by planting the same set of materials on the same day, but on different daylength treatments. In evaluating genetic materials for photoperiod sensitivity under extended daylength or long days alone will not be completely satisfactory, since maturity is confounded with photoperiod sensitivity. As a result, photoperiod sensitivity obtained by the difference of the extended and normal daylength values were used in the diallel cross analysis to partition out the effects of maturity. Such an approach to study photoperiod sensitivity is not totally unrealistic.

In the generation mean analysis study, it was unfortunate that maturity was confounded with photoperiod sensitivity since the crosses with the advanced populations were evaluated under extended daylength alone. Nevertheless, some information could still be obtained since the maturity genes and the photoperiod sensitivity "genes" were involved in the expression of flowering.

In this study, it was found that in general, insensitive x insensitive crosses produced insensitive genotypes. Crosses between insensitive and sensitive inbreds produced F_{1s} which were intermediate between their parental values, although they were still considered to be sensitive. Crosses between sensitive inbreds produced sensitive genotypes. These results were more or less consistent with the findings of Francis (1972a, 1972c).

In the diallel analysis, it was generally found that general combining ability was much more important than SCA in contributing to

the genetic variation of photoperiod sensitivity. The high narrow sense heritability estimates obtained suggest that conventional methods of recurrent selection such as backcrossing should be effective in converting tropical sensitive genotypes to low sensitivity. This was supported by the fact that the F_2 distributions were generally broad and bimodal in a few cases. Furthermore, most of the backcross populations to the sensitive parents showed early segregants which would also be insensitive genotypes. Thus photoperiod sensitivity in corn may be under the control of a few major genes as suggested also by Francis (1972a, 1972c) and Spencer (1974). Spencer (1974) also reported that the genes showed little or no dominance and there were indications that modifier genes were involved. The diallel analysis of Hayman and Jinks as well as the generation mean analysis using parents of comparable maturity have indicated that at least 1 to 2 genes with partial dominance controlled photoperiod in corn. In the cross between 11 Mex44 (sensitive) and Oh45r (insensitive), Spencer (1974) stated that this cross was under the control of 3 genes. This confirmed that photoperiod sensitivity in corn is simply inherited.

Scaling tests revealed the presence of epistasis in the genetic variation of days to anthesis in the generation mean analysis. This cannot be applied to photoperiod sensitivity as maturity is also confounded in the estimation. Furthermore, the test of homogeneity of the Wr - Vr statistics as well as the regression line in the graphical analysis have suggested the absence of epistasis in controlling photoperiod sensitivity.

The results from the generation mean analysis was similar to the results of Giesbrecht (1960a, 1960b), i.e. partial dominance for

earliness, presence of epistasis and 4 to 5 genes controlling flowering time. The genetic variance components were estimated on the assumption of the additive-dominance model, although some crosses were found to have epistatic components. According to Lawrence and Jinks (1973), the additive variance component would be underestimated, if the model used was inadequate since the estimates of V_A and V_D were inversely correlated. Nevertheless, narrow sense heritability estimates were still high in a great number of the cases.

Genetic interpretation on photoperiod sensitivity cannot be derived from the generation mean analysis with the confounding effects of maturity. As suggested earlier, one possibility of partitioning out the effects of maturity is to use sensitive and insensitive parental lines of comparable maturity. However, insensitive genotypes tend to be earlier, while sensitive genotypes tend to be later in maturity, although this is not entirely true. Another approach to this, is to plant a control under the short days. The population means computed under the short day conditions will reflect the maturity effects. Thus subtracting these means from the individual plant datum of the respective populations evaluated under long days will provide an estimate of photoperiod sensitivity effects. In the absence of a statistically suitable approach, the above technique is the next best solution to partition out the maturity effects. Future studies on generation mean analysis using this approach will have more meaningful results.

Varieties or races should also be considered for future studies with respect to photoperiod sensitivity. The variety, Gaspe Flint has been known to be the world's earliest corn (Brawn, 1963).

Similarly, the race, Zapolote Chico from Mexico was reported to be very early (Brown and Goodman, 1977). Whether these cultivars are essentially early or photoperiod insensitive in the true sense of the word requires some basic studies. According to Brawn (1963), Gaspe Flint flowered in about a month from planting with an average of 5 or 6 leaves. He also pointed out the possibility that tassel initiation had occurred in the seed of Gaspe Flint. Genetic and Basic physiological studies may provide a better understanding to its response to photoperiod.

Teosinte, a close relative of corn, is a short day plant which becomes profusely tillered and assumes an almost perrenial form of growth under continued long days (Mangelsdorf, 1974). However, short day treatments will bring it to flower (Emerson, 1924). Although teosinte crossed easily with corn, it is unlike corn since photoperiod sensitive corn will eventually flower under long days. Studies on this aspect may help contribute to a better understanding on the relationship of teosinte and corn.

Day-neutral teosinte was renamed as Northern teosinte since it was not truly insensitive to daylength (Galinat, 1970). According to him, Northern teosinte was selected among the progeny from a backcross to teosinte of the hybrid Guerrero teosinte x Gaspe Flint. However, in the initial screening here using growth chambers maintained at 12 and 16 hours, the meristem of Northern teosinte initiated (0.4 mm) 4 days after seedling emergence. This would indicate its photoperiod insensitivity. This unusual property of Gaspe Flint requires detailed study, especially its ability to transfer its earliness or photoperiod insensitivity.

Evaluation of the diallel cross under extended daylength in Hawaii and under long days in Illinois showed consistent results with some exceptions. Tx601 as well as the hybrid CM104 x Tx601 flowered earlier in Illinois than in Hawaii. The inbred CM104 was not affected to the same degree. This was due to the fact that in Illinois, the daylength was decreasing while in Hawaii the daylength was kept almost constant for the duration of growth. As shown in Section 4, tassel initiation of Tx601 was delayed more under 16 hour than 14 hour daylength. This showed that Tx601 had a longer daylength requirement than CM104 for delayed flowering. The fact that CM104 x Tx601 behaved similarly as Tx601, and having almost comparable sensitivity difference appeared to indicate that daylength requirement for delayed flowering is under genetic control. Some studies of this nature will enlighten the subject of photoperiod sensitivity and may have possible benefits for regions having intermediate daylengths.

In conclusion, photoperiod sensitivity is not as complex as it seems to be. It is highly heritable and under the control of a minimum of 2 genes showing partial dominance. Selection for low sensitivity will progress rapidly under the appropriate daylength conditions.

7. COMBINING ABILITY OF YIELD AND YIELD COMPONENTS

7.1 10 x 10 Diallel Cross

A 10 entry diallel cross was evaluated for two seasons. One planting was made on November 4, 1976 and the other on March 15, 1977. These were referred to in this study as the winter and summer plantings respectively. The experimental design used was randomized complete block design with three replicates. Analysis of variance of grain yield and its yield components, i.e. cob length, kernels per row and 100 kernel weight showed that genotypes were significantly different ($P = 0.01$) when evaluated at the two seasons (Table 46). The coefficient of variation was only slightly higher in winter than in summer. This was due to the unusual winter experienced that year, with warmer days, lower rainfall, and fewer cloudy days than expected. Combined analysis of the two seasons (Table 47) was also carried out for all the characters studied. Season significantly affected the characters studied. Genotypes as well as the genotype by season interaction were also highly significant. This would indicate that certain genotypes performed differently in the two seasons.

Hybrid and parental means of grain yield, cob length, kernels per row and 100 kernel weight for the two seasons are presented in Table 48 and in Appendices 7, 8 and 9 respectively. Lower grain yield was obtained in the winter than in the summer planting for all genotypes in the diallel cross. This was also true for all the other yield components studied. This could be easily visualized by looking at the array means for the two seasons.

Table 46. Analysis of variance of yield and yield components of a 10-entry diallel cross evaluated at two seasons

Source	df	Mean squares			
		Grain yield	Cob length	Kernels per row	100 kernel weight
Winter					
Replicate	2	0.11	2.85*	6.52	2.73
Genotypes	54	5.52**	9.84**	86.75**	35.53**
Error	108	0.37	0.78	7.36	5.83
CV%		16.00	7.57	11.16	11.54
Summer					
Replicate	2	24.22**	11.18**	70.69**	47.64**
Genotypes	54	20.30**	10.50**	123.63**	54.82**
Error	108	1.30	0.91	6.54	5.57
CV%		13.52	5.81	7.68	7.84

Table 47. Combined analysis of variance for grain yield and yield components of a 10-entry diallel evaluated in two seasons

Source	df	Mean squares			
		Grain yield	Cob length	Kernels per row	100 kernel weight
Season (S)	1	1738.81**	1828.07**	6615.17**	6969.01**
Reps in S	4	12.16	7.02	38.60	25.18
Genotype (G)	54	21.98**	18.20**	191.95**	71.16**
G x S	54	3.84**	2.13**	18.43**	19.18**
Error (b)	216	0.84	0.84	6.95	5.70

Table 48. Grain yield (metric tons/ha) of the 10-entry diallel at two seasonal planting

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601	Array mean
Va35	1.70[a]	3.42	2.98	2.77	2.22	4.54	2.97	4.63	5.59	4.14	3.50
	3.96	5.85	8.25	5.15	8.10	7.46	7.05	8.44	10.22	11.67	7.62
A619		0.90	4.41	1.76	3.80	3.43	4.64	3.79	5.81	5.14	3.71
		3.35	7.91	4.80	8.86	6.95	9.82	9.01	10.74	13.73	8.10
B37			1.40	3.53	3.27	2.45	3.82	4.03	5.19	4.97	3.61
			3.36	7.45	7.98	7.28	9.75	9.97	10.90	11.52	8.44
Oh43				1.92	3.25	3.99	3.47	3.80	5.12	5.07	3.47
				3.59	8.20	9.29	9.62	9.17	11.88	11.11	8.03
Mo17					1.48	3.44	3.52	2.84	4.71	5.04	3.36
					5.08	7.66	10.67	6.93	10.98	10.70	8.52
Hi25						1.84	4.30	5.16	5.99	5.10	4.02
						3.14	7.93	8.73	10.83	9.35	7.86
Hi26							1.86	5.81	5.80	5.16	4.14
							6.00	10.52	11.87	10.92	9.42
Hi30								3.23	5.15	5.30	4.37
								5.22	10.69	10.78	8.95
CM104									2.80	5.90	5.21
									8.38	10.60	10.71
Tx601										2.27	4.81
										3.78	10.41

[a] Upper and lower values represent Winter, 1976 and Summer, 1977 respectively

BLSD (0.05) = 0.89 Mean heterosis % = 123.28
1.65 105.77

The hybrid with the highest grain yield in the winter planting was Hi25 x CM104. However, the best hybrid in the summer was A619 x Tx601, although its yield was also comparatively high in winter. This reflected the differential response of the different genotypes under different environments, which had brought about the highly significant genotype x season interaction.

Generally, hybrids involving CM104 and Tx601 had relatively higher yields under winter and summer conditions. This was also true in the case of cob length and 100 kernel weight, but not necessarily so for kernels per row, although they were also high. Mean heterosis percentage was calculated for all the characters, and it was found that they were higher in the winter plantings than the summer except for 100 kernel weight.

The mean grain yield was computed over the two seasons (Appendix 10) to provide an indication of the superiority of genotypes over the different environments. The best hybrid was A619 x Tx601. The means of the hybrids showed that in general, any crosses with CM104 and Tx601 would perform well in both environments.

The percentage yield reduction of the winter planting as compared to the summer planting was computed for the hybrids and their parental lines (Table 49). This was the difference of the yield under the two seasons divided by the yield of the summer planting and expressed in percent. There was a wide variation in percentage yield reduction from 38.1 for Hi30 to 73.1 for A619. This happened to be inbred lines. In considering only the hybrids, yield decreased 39.1% for Va35 x Hi25 while it was decreased 72.6% for Va35 x Mo17. Overall inbreds and their hybrids yield was reduced by 54.5%. It must be pointed out that a small

Table 49. Percent grain yield reduction of winter planting as compared to summer

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601	Array mean
Va35	57.1	41.5	63.9	46.2	72.6	39.1	57.8	45.1	45.3	54.1	52.3
A619		73.1	44.2	63.3	57.1	50.6	52.7	57.9	62.5	54.2	55.7
B37			58.3	52.6	59.0	66.3	60.8	59.6	52.4	56.8	57.4
Oh43				46.0	60.4	57.1	63.9	58.6	56.9	54.4	55.9
Mo17					70.9	55.1	67.0	59.0	57.1	52.9	61.1
Hi25						41.4	45.8	40.9	44.7	45.4	48.6
Hi26							69.0	44.8	51.1	52.7	56.6
Hi30								38.1	51.8	50.8	50.7
CM104									66.6	44.3	53.3
Tx601										39.9	50.6

Mean percentage reduction = 54.4%

reduction might not necessarily mean a high yield was obtained when a particular genotype was grown in summer or winter. The result merely indicates the stability of the genotype under the different environments.

Combining ability analyses (Griffing, 1956) were carried out for all the characters studied under the two seasons (Table 50). General combining ability (GCA) and specific combining ability (SCA) mean squares were highly significant for all characters in both seasons. This indicated that additive and non-additive genes contributed to the genetic variation of grain yield, cob length, kernels per row and 100 kernel weight regardless of season. GCA/SCA ratio was more than unity for all cases suggesting that GCA was more important than SCA in the genetic contribution. With the exception of kernels per row, the GCA/SCA ratio was larger for all characters planted in winter than in summer.

In the combined analysis (Table 51), GCA and SCA mean squares were also found to be highly significant for all the characters. The GCA x season interaction as well as the SCA x season interaction was also highly significant. This would suggest that both additive and non-additive genes were not stable in their expression under different environments.

Estimates of GCA effects under the two seasons were calculated for all the characters (Table 52). Generally all the temperate inbreds did not combine as well as the tropical inbreds under the two seasons in Hawaii. High positive GCA effects were obtained for CM104 and Tx601 for grain yield at the two seasons. This would suggest that these two inbreds were good combiners for grain yield in summer and in winter.

Table 50. Mean squares for general and specific combining abilities and error of grain yield and its yield components at two seasons

	GCA	SCA	GCA/SCA	Error
Winter 1976				
Grain yield	3.74**	1.46**	2.56	0.12
Cob length	8.42**	2.25**	3.74	0.26
Kernels/row	46.22**	25.46**	1.82	2.45
100 kernel wt.	48.60**	4.50**	10.81	1.94
Summer 1977				
Grain yield	11.72**	5.78**	2.03	0.43
Cob length	4.95**	3.21**	1.54	0.30
Kernels/row	74.35**	34.59**	2.15	2.17
100 kernel wt.	46.09**	12.71**	3.63	1.85

Table 51. General and specific combining ability mean squares of grain yield and yield components combined over the two seasons (S)

	Grain yield	Cob length	Kernels per row	100 kernel wt.
GCA	6.862**	5.815**	54.755**	42.691**
SCA	3.099**	2.479**	27.446**	5.699**
GCA x S	8.593**	7.550**	69.148**	51.998**
SCA x S	4.139**	2.983**	27.168**	11.509**
Error	0.278	0.281	2.311	1.895

Table 52. Estimates of GCA effects of grain yield and its yield components at two seasons

Inbreds	Grain yield		Cob length		Kernels/row		100 kernel wt.	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Va35	- 7.59	-17.35	-0.71	-0.56	-2.20	-1.16	-0.41	-2.28
A619	- 5.76	-11.52	-1.17	-0.81	-3.42	-3.80	0.18	-0.26
B37	- 6.49	- 6.78	-1.04	-0.28	-1.77	-1.01	1.48	0.45
Oh43	- 7.63	-12.17	-0.63	-0.66	-0.34	-0.52	-2.44	-2.20
Mo17	- 9.83	- 3.31	0.01	0.79	2.04	4.40	-3.82	-1.86
Hi25	- 0.06	-15.08	0.61	-0.07	-0.52	-3.21	0.38	-0.45
Hi26	1.52	10.43	0.37	0.30	1.99	2.24	-0.25	-0.15
Hi30	6.72	2.86	0.63	-0.12	1.21	0.32	0.24	0.36
CM104	17.70	31.71	1.25	1.19	1.07	1.70	3.42	3.08
Tx601	11.43	21.21	0.69	0.22	1.95	1.05	1.20	3.31
S.E. $(g_i - g_j)$	2.40	4.47	0.21	0.22	0.64	0.60	0.57	0.55

In the case of cob length, highest GCA effects were again obtained for CM104 under the two seasons. As for Tx601, GCA effects were high in winter but not in summer. Mo17 did not combine well for cob length when evaluated under the winter months, but it was a good combiner when evaluated in summer.

The tropical inbreds were not as good combiners as some temperate inbreds for kernels per row, even though positive GCA effects were still obtained. Mo17 and Hi26 showed consistently high positive GCA effects for this character under the two seasons, with Mo17 being the best combiner.

The inbred CM104 again showed the high GCA effects for 100 kernel weight for both seasons. Tx601 was a good combiner for this character in summer, but comparatively poorer than CM104 in winter.

Estimates of SCA effects were also computed for all the characters. With some exceptions, the SCA effects in the crosses involving CM104 or Tx601 as inbreds were positive and high in both seasons (Appendix 11). The hybrid with the highest SCA effects in the winter planting was Hi26 x Hi30. A619 x B37 and A619 x CM104 were the other two which had good hybrid combinations for yield under the winter conditions. In the summer planting, the hybrid A619 x Tx601 had the highest SCA effects indicating that non-additive genes for grain yield were better expressed in the summer than in winter. Other crosses which had good hybrid combinations for yield in the summer were Va35 x Tx601, B37 x Tx601, Oh43 x Hi25, Oh43 x CM104, Oh43 x Tx601 and Mo17 x Hi26.

SCA effects for cob length (Appendix 12) showed that the hybrids with very high and positive SCA effects in the winter evaluation were

A619 x Mo17 and Va35 x CM104. In the summer evaluation, the hybrid A619 x Tx601 showed the highest SCA effects for cob length, as was also the case for grain yield. B37 x Hi30 was the other hybrid which had high SCA effects for cob length in the summer season.

In the case of kernels per row (Appendix 13), among the hybrids with very high SCA effects were Va35 x CM104, A619 x B37, A619 x Mo17 and Mo17 x Hi26, when evaluated in the winter months. Hybrids with high SCA effects in the summer planting were Va35 x Tx601, A619 x Tx601, B37 x Tx601, Mo17 x Hi26 and Hi25 x Tx601.

Appendix 14 showed the SCA effects of 100 kernel weight of the two season plantings. A619 x Hi25, B37 x CM104, Mo17 x Tx601 showed high SCA effects for 100 kernel weight in the winter planting. In the summer planting, high SCA effects were expressed by A619 x Tx601, Oh43 x Hi25, Oh43 x Tx601 and Mo17 x CM104.

These results indicated that the hybrids which made full use of non-additive genes for expression of the various characters were not the same for the two seasons and for the different characters. Exceptions to this occurred especially A619 x Tx601 where SCA effects in general were consistently high for all the characters under the summer evaluation. The hybrid Mo17 x Hi26 also showed consistent high SCA effects for kernels per row under winter and summer, indicating that the expression of the non-additive genes for this hybrid was rather stable for this character.

Heritability estimates were also calculated for all these characters (Table 53) on the assumption of the random model. Narrow sense heritability estimates for both seasons were much lower than the broad

Table 53. Narrow and broad sense heritability estimates of grain yield and yield components at two seasons

Characters	nh^2		bh^2	
	Winter	Summer	Winter	Summer
Grain yield	20.6	14.6	93.2	93.6
Cob length	31.3	8.3	92.1	91.4
Kernels/row	12.0	16.1	91.5	94.7
100 kernel wt.	62.1	30.4	83.6	89.9

sense heritability indicating that the SCA component did play a significant role in contributing to the genetic variation of these characters. In comparing the seasonal effects, narrow sense heritabilities were higher in winter than in summer in all cases except kernels per row. This would tend to suggest that selection for grain yield and yield components using methods which relied on additive genetic variation would be faster in the winter conditions. Broad sense heritability did not differ greatly under the two seasons.

7.2 Discussion

The yield performance of the hybrids and their parental lines was greatly reduced in the winter planting as compared to the summer. The average percent reduction in yield was found to be 54.4%. This yield reduction could be attributed mainly to low light intensity as well as shorter light duration. The means of light intensity, temperature and light duration over the three months of the plants' growth were 270.5 langleys per day, 22.8^{o}C and 11.04 hours respectively for the winter planting. In the case of the summer planting, the means were 383.6

langleys per day, 22.8°C and 12.34 hours respectively. There was a 29.5% drop in light intensity and 10.5% drop in duration of light on the average, but there was no change in temperature on the whole. This was due to the unusually warm and dry winter experienced that year thereby demonstrating the significance of light as a major factor affecting yield as has been frequently reported in the literature.

Yield components were similarly affected by this reduction in light. However, reduction in yield and its yield components for all the genotypes were not proportional, as was evident in the significant genotype x season interaction obtained for all characters. Since both plantings were irrigated by an overhead sprinkler system, rainfall values were not mentioned initially. Nevertheless it would be wrong to intimate that rainfall had no effects on the significant interaction. Generally, it is wetter in the winter months, and coupled with the cloudy conditions, it sets the conditions for high disease and insect infestations. Similarly temperature is also of importance in affecting yield. These complex interactions of factors of which light is of major importance constitutes the environment whether favorable or unfavorable for the plants' growth.

Percentage yield reduction would tend to indicate the relative stability of the various genotypes over the two contrasting environments. There was no consistent trend to indicate that the hybrids were more stable than the inbred lines. In fact, the lowest and the highest percent yield reduction were inbreds, Hi30 and A619 respectively. Thus both inbreds and the single crosses are genetically homogenous populations and will have to rely heavily on "individual buffering" (as termed by Allard and Bradshaw, 1964) for yield stability. On the other hand, a

variety which is a heterogenous population will possess what is called a "population buffering."

Sprague and Federer (1951) showed evidence that double crosses had less interaction with the environment than single crosses. This apparently suggested that double crosses were more stable than single crosses. Similar results were also obtained by Eberhart and Russell (1969) in comparing double and single crosses, and with Wright et al. (1971) in three-way and single crosses.

Combining ability analyses have indicated the significance of both GCA and SCA in contributing to the genetic variation of grain yield and its yield components in both seasons. The GCA/SCA ratio which was greater than unity in all cases suggested additive genes predominate in the genetic variation. However both the additive genes and the non-additive genes were not stable in their expression for yield and yield components as indicated by the highly significant GCA x season and SCA x season interactions. Eberhart and Russell (1966, 1969) however reported that the additive genes were the primary cause of the genotype-environmental interactions from their diallel crosses. It must be pointed out that their evaluations were based on different environments of the same season, i.e. summer whereas the studies here were based on different environments, and of different seasons.

The tropical inbreds especially CM104 and Tx601 have good combining abilities for grain yield in both seasons as compared to the temperate inbreds. This may only apply to the different environments in Hawaii or possibly other parts of the tropics as well. In fact some of the temperate inbreds such as Mo17, B37 and A619 were rated as among the top 4 inbreds (Zuber, 1975) commonly used in hybrid combinations in the

Corn Belt. Most of the outstanding yield performances in both seasons were shown by temperate inbred x tropical inbred, especially the crosses involving the two tropical inbreds CM104 and Tx601. These crosses may have high individual buffering in view of the fact that they have constituents from the two distinct regions of adaptation. Undoubtedly, use of tropical germplasm in crosses with temperate genotypes should be favored to exploit its yielding capacity, even in the Corn Belt. This may be likely if the tropical genotypes are converted to low photoperiod sensitivity (Section 6).

Narrow sense heritability estimates were generally higher in the winter than in summer except kernels per row. Nevertheless, this indicates that it will be advantageous to select for yield over different environments or seasons for which the hybrids or varieties are being developed. This will result in the development of a hybrid or variety which will perform well in different environments.

In the tropics or subtropics, corn can be grown throughout the year and, as such, seasonal effects are of importance. This differed greatly from the effects of different environments as referred to in the Corn Belt. Temperate corn breeders will tend to develop hybrids or varieties which are stable over a wide range of environments. However, the type of variation in the different environments is not as drastic as the seasonal variation. Although there is a tendency for breeders to develop a hybrid or variety for all seasons, it may be worthwhile having hybrids or varieties tailored for the specific seasons. As suggested by Comstock and Moll (1963) in reference to environments, the first approach is favored by small genotype-environmental interactions and the second by large.

8. EFFECTS OF PLANTING DATES ON AGRONOMIC CHARACTERS

8.1 Monthly Plantings

Six hybrids were planted every month for a period of twenty months starting from October, 1975 at the Waimanalo Research Station. These were replicated twice and planted in a randomized complete block design. Data on solar radiation (langleys per day) and maximum and minimum air temperature were recorded during the period that the study was carried out. The monthly means are graphed in Figure 21. Daylength (from sunrise to sunset) or light duration was also graphed as monthly means which were computed from the table of sunrise and sunset at Honolulu, published by the Nautical Almanac Office, United States Naval Observatory, 1959.

The two winter seasons were characterized as having relatively lower levels of solar radiation, maximum and minimum temperatures and shorter daylength (Figure 21). The observed values increased progressively through spring with the highest values of solar radiation and temperature and the longest daylength during the summer months. The six hybrids planted monthly for twenty months were exposed to this cyclical variation in climate.

Analysis of variance was conducted for the usual plant and ear characters studied for all the twenty plantings. The results of the individual analysis of variance are summarized in Appendix 15. Hybrids differed significantly in all months, but the plantings in April, June, August, October, 1976 and May, 1977. Planting in these months may have subjected the plants to high solar radiation, high maximum and minimum temperature, as well as longer light duration. It therefore

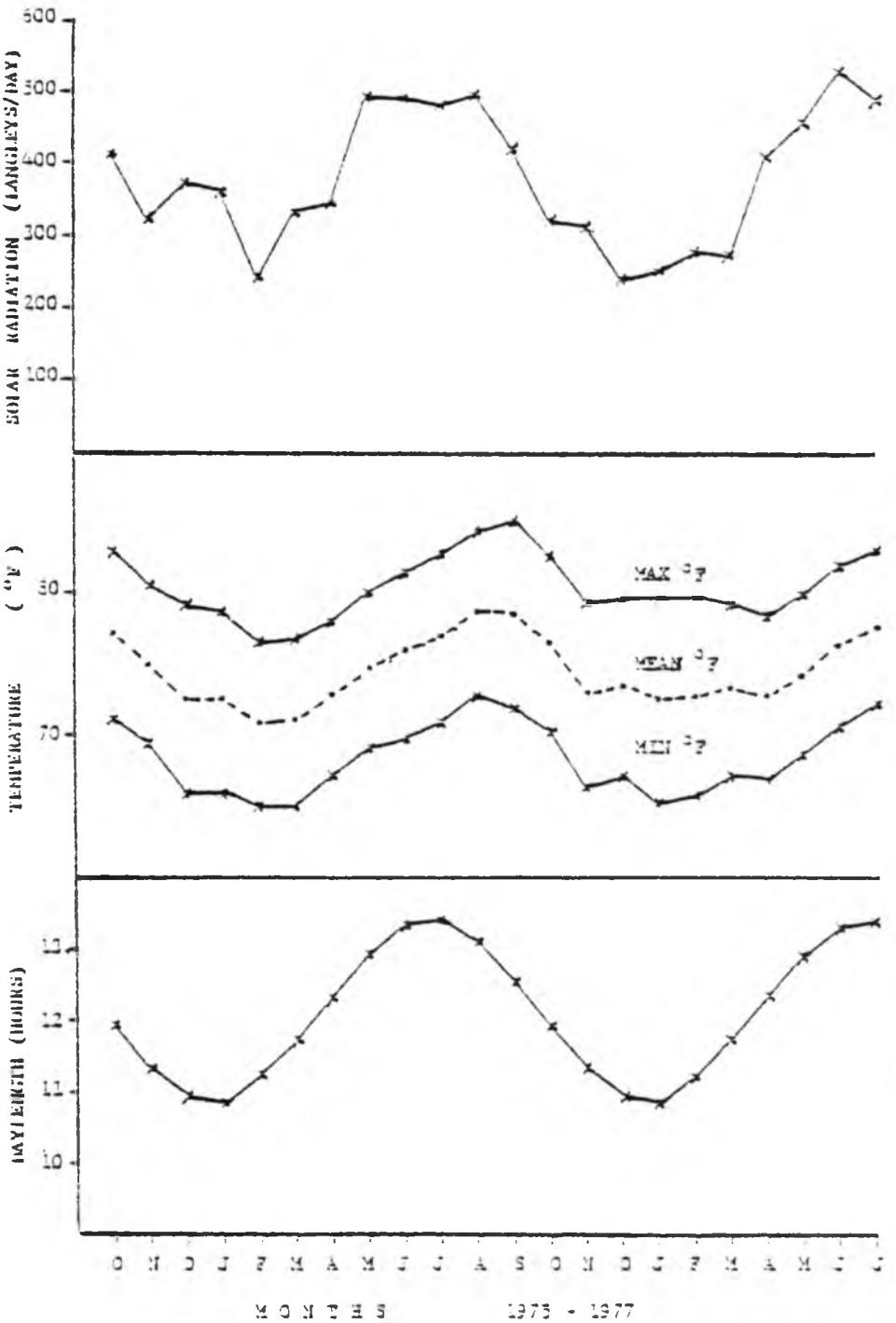

Figure 11. Monthly mean solar radiation, temperature and daylength from October 1975 to July 1977 for Waimanalo, Hawaii

appeared that under optimum conditions of growth, hybrids tend to differ less for days to mid-silk.

Plant height (Appendix 15) among the hybrids were not significantly different in the majority of the monthly plantings. There were a few months in which significant differences occurred. Ear height however did differ significantly among the hybrids for almost all the months indicating that ear height differences among the hybrids occurred regardless of climate.

There were only a few months where significant differences in cob length, filled ear length and row number were observed among the hybrids. Where significant differences did occur, they were usually associated with low solar radiation, lower temperature and shorter daylength. From January to May, 1976, the six hybrids did not differ in these three characters. Significant differences however occurred among these hybrids from January to April, 1977 for cob length and filled ear length, and from February to April, 1977 for row number. These differences in results may be attributed to variations in climate from year to year.

Kernels per row, ear weight and grain yield were generally found to differ significantly among hybrids. However, in several of these months, no significant differences were found. Similarly, this was also found to be so for the 100 kernel weight and kernel depth.

It must be pointed out that with only 5 degrees of freedom for error in the individual analysis due to few replications, error mean squares would tend to be large. Unless hybrid differences were great, non significance would be detected most of the time.

A combined analysis of variance of the twenty planting dates was carried out for all the characters studied (Table 54). Highly

Table 54. Analysis of variance of agronomic characters for 6 corn hybrids over the 20 planting dates

Source	df	Days to mid-silk	Plant height	Ear height	Cob length	Filled ear length
Dates (D)	19	442.33**	13433.69**	5080.50**	76.12**	90.92**
Reps in D	20	2.35	250.24	142.13	2.15	2.06
Hybrids (H)	5	369.31**	5454.14**	9452.56**	53.28**	60.84**
H x D	95	4.89**	212.98**	123.63**	2.40*	3.50**
Error (b)	100	2.36	111.85	52.05	1.73	2.12

Source	df	Row no.	Kernels per row	Ear weight	Grain yield	100 kernel wt.	Kernel depth
Dates (D)	19	5.85**	488.05**	24162.30**	64.41**	58.23**	0.026**
Reps in D	20	0.66	12.95	1379.36	3.51	10.93	0.002
Hybrids (H)		20.45**	948.14**	44176.15**	119.04**	183.03**	0.145**
H x D	95	0.88*	24.39**	1383.12**	3.83**	15.34**	0.004**
Error (b)	100	0.60	11.20	524.93	1.41	5.03	0.002

significant differences were found for planting dates as well as for hybrids. The hybrid x dates interaction was also significant or highly significant for all the characters studied. This indicated that the various hybrids had a differential response to planting dates or rather the changing climatic conditions.

A general mean of all the hybrids for each planting is presented for all the characters studied (Table 55). The results indicate the least and most favorable planting dates for corn production in Hawaii. The trend in days to mid-silk showed that corn flowered later in the winter months and progressively earlier thereafter. Flowering was earliest in the summer months when the days were longest and had higher temperatures and solar radiation. The results clearly demonstrated that photoperiod was not long enough in Hawaii to cause delays in flowering otherwise corn, a short-day plant, would flower late in the summer than in the winter months. The results of this study showed that early or late flowering would be a function of environmental factors other than photoperiod. Plant and ear height were found to be much shorter in the winter months. Plants became progressively taller under the warm, bright and long summer days.

Grain yield and yield components (Table 55) were also cyclical with climate, with the best performance in the summer months and the worst in the winter months. Looking specifically at grain yield, performance was drastically reduced by planting in November, 1975 to January, 1976 and from October, 1976 to January, 1977. Thus, planting in February onwards to September of each year would result in good yields as compared with planting in the months from October to January.

Table 55. Mean response of 6 hybrids for several agronomic characters at 20 planting dates

Planting dates	Days to mid-silk	Plant height (cm)	Ear height (cm)	Cob length (cm)	Filled ear length (cm)	Row no.
Oct 75	66.2	170.7	62.6	15.5	12.8	14.6
Nov 75	69.0	196.0	72.0	13.7	9.9	13.7
Dec 75	70.3	162.1	69.6	13.1	11.2	13.1
Jan 76	69.8	178.4	61.4	12.6	10.0	12.8
Feb 76	66.2	188.6	70.1	15.4	12.9	13.9
Mar 76	63.1	213.8	92.6	17.5	15.4	14.5
Apr 76	58.2	203.9	89.4	18.4	16.3	14.4
May 76	60.0	218.2	97.1	18.9	17.1	14.8
Jun 76	53.8	240.8	122.6	19.4	17.6	14.9
Jul 76	53.2	268.4	120.8	17.8	15.7	14.6
Aug 76	48.8	274.0	119.6	17.2	14.8	14.7
Sep 76	54.7	217.6	91.9	15.4	12.3	14.3
Oct 76	62.2	190.6	70.2	12.4	9.6	13.1
Nov 76	66.8	153.2	60.0	11.7	9.2	13.2
Dec 76	61.8	208.2	82.4	12.1	9.6	13.6
Jan 77	59.9	200.7	85.7	13.3	11.1	14.4
Feb 77	60.0	209.7	84.1	16.2	14.0	14.4
Mar 77	61.9	233.5	93.1	16.1	13.9	14.5
Apr 77	57.3	250.8	111.9	17.8	15.8	15.0
May 77	52.2	245.5	113.3	18.5	15.7	15.0
BLSD (0.05)	1.1	11.3	8.5	1.0	1.0	0.6

Table 55. (Continued) Mean response of 6 hybrids for several agronomic characters at 20 planting dates

Planting cates	Kernels per row	Ear weight (gm)	Grain[a] yield	100 kernel weight (gm)	Kernel depth (cm)
Oct 75	27.7	147.5	7.42	31.4	1.09
Nov 75	20.9	100.7	4.80	26.7	1.04
Dec 75	19.8	106.1	5.13	29.7	1.05
Jan 76	21.7	96.7	4.72	24.5	1.01
Feb 76	30.3	150.0	7.39	27.2	1.05
Mar 76	32.1	179.3	8.87	27.8	1.08
Apr 76	34.6	215.8	10.84	29.4	1.10
May 76	37.2	216.2	11.00	26.6	1.14
Jun 76	36.0	217.8	10.85	29.5	1.12
Jul 76	33.5	209.9	10.35	32.0	1.16
Aug 76	31.3	190.5	9.73	34.0	1.19
Sep 76	27.6	142.1	7.24	30.6	1.12
Oct 76	22.4	108.8	5.44	29.5	1.08
Nov 76	20.1	90.1	4.43	27.6	1.06
Dec 76	22.4	105.8	5.28	28.6	1.06
Jan 77	24.4	120.8	5.84	27.7	1.03
Feb 77	33.4	178.2	9.00	31.2	1.13
Mar 77	33.3	177.4	8.80	31.1	1.11
Apr 77	38.0	193.6	9.95	29.8	1.12
May 77	37.6	178.8	8.98	29.1	1.12
BLSD (0.05)	2.6	26.9	1.35	2.6	0.03

[a] Grain yield is expressed in metric tons/ha

Planting in May, 1976 resulted in the highest corn yield which had on the average 11 metric tons per hectare. Plantings made in April, June, July and August, 1976 also produced high yields which were not significantly different from the yield of the May planting. The May planting in 1977 however did not produce the highest yield and was significantly lower than the May planting of 1976. The variations in yield may have been due to climatic variations between years or to other factors not measured.

Superior hybrids could be identified by the average performance over the twenty months of planting. The hybrid means over the twenty months for all the characters are listed in Table 56. As stated previously, significant differences occurred among the hybrids for all characters in the combined analysis (Table 54). If hybrid superiority is defined in terms of yield, then hybrid means for yield and yield components are of more importance than days to mid-silk, plant height and ear height (Table 56). Also, differences exhibited by the hybrids for the latter three characters were not great in most cases.

The hybrid with the highest mean yield over the twenty months was H763 followed by H652 and H816 (Table 56). The hybrid H763 also had the highest mean values for all the yield components studied except row number. The differential response in yielding performance would best be seen in Figure 22 where the mean grain yield of each hybrid was plotted against time of planting. The hybrid H763 had the highest yield in most months followed by H816 and H652. In certain instances H816 or H652 outperformed the other hybrids. In the July and August, 1976 plantings, H816 had higher yield than H763 and H652. In the September, 1976 planting both H816 and H763 were the highest yielders.

Table 56. Hybrid means of several agronomic characters averaged over the 20 monthly plantings

Characters	H652	H763	H787	H814	H815	H816	BLSD (0.05)
Days to mid-silk	59.6	60.6	59.1	56.4	63.0	65.1	0.6
Plant ht. (cm)	209.2	214.8	201.8	196.4	215.4	229.7	4.1
Ear ht. (cm)	88.0	93.9	76.9	65.0	104.9	102.5	2.8
Cob length (cm)	16.4	17.5	15.2	14.1	15.2	15.5	0.5
Filled ear length (cm)	14.5	14.5	12.2	11.5	13.0	13.8	0.6
Row no.	15.2	13.6	13.2	14.2	14.7	14.3	0.3
Kernels per row	32.7	34.3	24.8	22.0	29.3	32.2	1.3
Ear wt. (gm)	170.2	198.2	127.3	109.2	154.2	178.8	8.9
Grain yield[a]	8.8	10.0	6.3	5.4	7.6	8.8	0.1
100 kernel weight (gm)	28.3	32.5	31.0	26.8	27.9	28.6	0.9
Kernel depth (cm)	1.10	1.19	1.10	1.02	1.04	1.11	0.02

[a] Grain yield is expressed in metric tons/ha

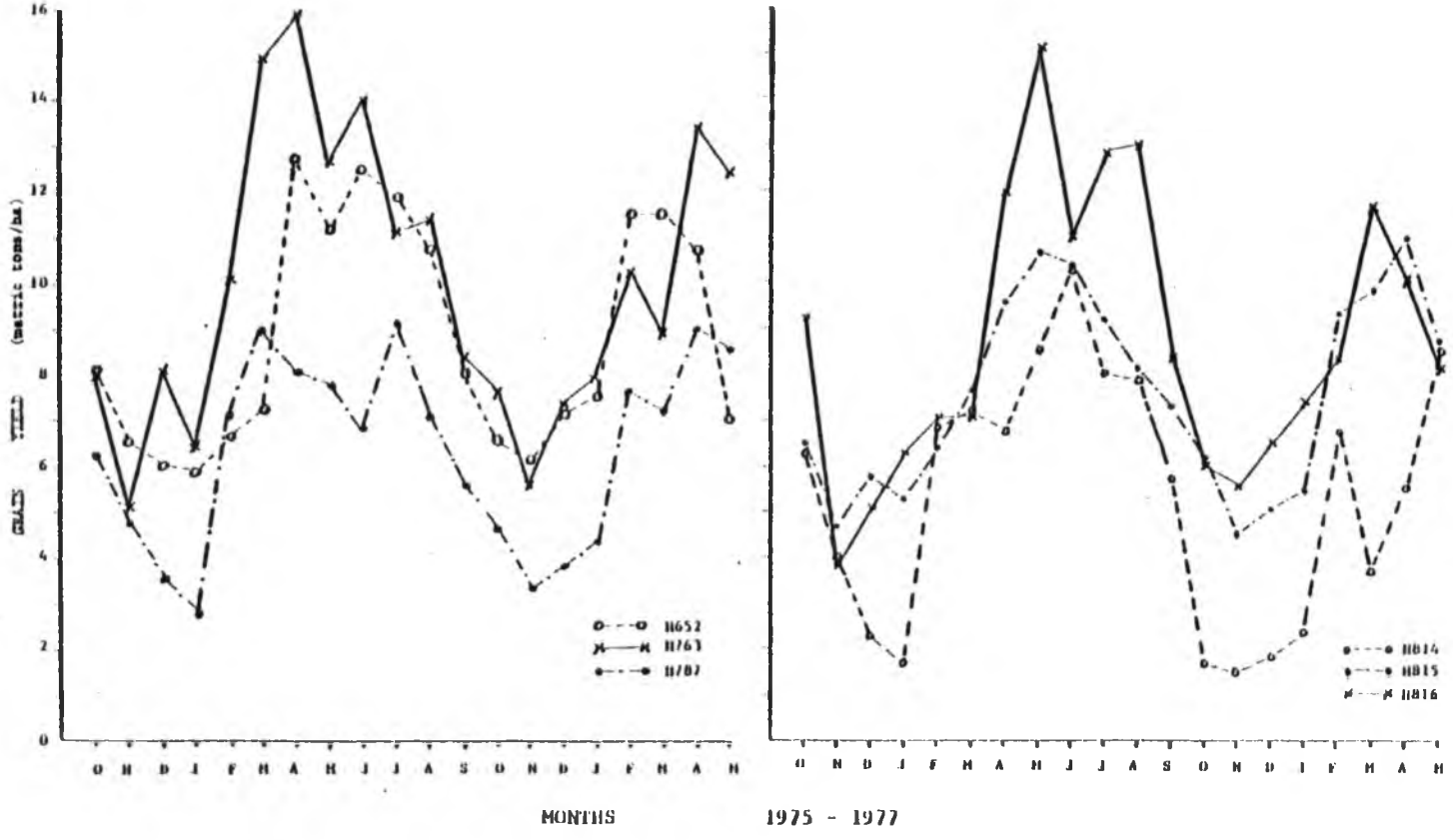

Figure 22. Mean grain yield of six hybrids planted monthly from October 1975 to May 1977

The hybrid H814 had on the average the lowest yield performance as well as the lowest values for most of its yield components (Table 56).

The response of the six hybrids to the twenty planting dates are listed for grain yield and its yield components, cob length, row number, kernels per row, 100 kernel weight, and kernel depth in Appendices 16, 17, 18, 19, 20 and 21 respectively. Since the data for filled ear length and ear weight were similar to cob length and grain yield respectively, they were not presented.

8.2 Effects of Climatic Factors on Corn

Multiple regression analyses were carried out using meteriological data collected at the Waimanalo Research Station and such agronomic characters as grain yield, cob length and days to mid-silk. The agronomic characters were used as Y variables in separate analyses, and mean solar radiation, mean maximum and minimum temperature, and daylength were the X variables. Mean solar radiation in langleys per day was computed for three month periods covering the active growth period of the corn plant except the analysis involving days to mid-silk or unless otherwise stated. Similar means were calculated for temperature as well as daylength. Multiple regression analyses were conducted on an individual hybrid basis, since hybrid x dates interaction in the combined analysis of variance (Table 54) was found to be significant.

In the analysis using days to mid-silk as the dependent variable, the mean values of the independent variables such as solar radiation, maximum and minimum temperatures, and daylength were average over the first two months of the plant's growth. This was because flowering would have occurred after two months in most cases. Days to mid-silk were highly and negatively correlated with each of these climatic

factors in all the hybrids (Table 57).

The partial regression coefficients (b_i) in relation to days to mid-silk are shown in Table 58. Missing values for certain climatic variables in the regression equation would mean that their effects were small and non-significant as tested by the partial F-value when these variables were entered into the equation for computation. The magnitude of b_i would not indicate which climatic variable would be the most or least important since the climatic variables were of different measurements.

In all the hybrids studied, all the climatic factors were important in influencing days to mid-silk except minimum temperature in H814 and H815, and solar radiation in H816 (Table 58). The b_i for solar radiation was positive suggesting that the higher the solar radiation, the later the plants would flower. This was not the case from the observed data on days to mid-silk, and furthermore, there was a negative correlation between days to mid-silk and solar radiation (Table 57). This conflicting result may be due to the high correlation between solar radiation and daylength ($r = 0.93^{**}$). The b_i for maximum temperature indicated that the higher the day temperature the faster the development of the plant resulting in earlier flowering. In the case of minimum or night temperature, the b_i was positive, but the correlation coefficient between days to mid-silk and minimum temperature was negative (Table 57). This may also be attributed to the high correlation between maximum and minimum temperatures. The b_i for daylength was negative suggesting that the longer the daylength the earlier the flowering. This again suggested that daylength variations in Hawaii are not great enough to cause delays in flowering through photoperiod

Table 57. Correlation coefficients between days to mid-silk and several climatic factors for the 6 hybrids

	H652	H763	H787	H814	H815	H816
Langleys/day	-0.59**	-0.63**	-0.64**	-0.60**	-0.69**	-0.60**
Max ^{o}F	-0.66**	-0.73**	-0.71**	-0.66**	-0.74**	-0.73**
Min ^{o}F	-0.67**	-0.74**	-0.74**	-0.70**	-0.78**	-0.71**
Daylength	-0.77**	-0.78**	-0.81**	-0.74**	-0.80**	-0.73**

Table 58. Partial regression coefficients between days to mid-silk and several climatic factors for the 6 hybrids

	H652	H763	H787	H814	H815	H816
Langleys/day	0.038	0.036	0.045	0.044	0.036	--[a]
Max ^{o}F	-3.309	-3.075	- 2.894	-1.172	-1.548	-4.781
Min ^{o}F	2.974	2.319	2.114	--	--	4.290
Daylength	-9.661	-8.871	-10.082	-7.226	-7.591	-7.875
Constant	224.460	242.389	251.530	220.832	265.123	251.031
Multiple R	0.92**	0.93**	0.94**	0.84**	0.89**	0.90**

[a] not selected

effects. The multiple correlation was highly significant indicating that the climatic variables in the regression equation significantly influenced days to mid-silk. The square of this multiple correlation would indicate the amount of variation in the dependent variable, i.e. days to mid-silk which was accounted for by the independent variables.

High correlation coefficients between any two independent variables would tend to provide a poor estimate of b_i for the variable that was entered into the equation last. Thus, if one variable did not enter into the equation because its effects were reduced by being highly correlated with another variable in the equation, this would not mean that the variable not in the equation was not important. Using the monthly means of the climatic factors averaged over the three months, a correlation matrix was set up (Table 59). Among the four climatic variables, it was found that daylength was highly correlated with solar radiation, and that maximum temperature was also highly correlated with minimum temperature.

Table 59. Correlation coefficients among several climatic factors

	Max ^{o}F	Min ^{o}F	Daylength
Langleys/day	0.59**	0.80**	0.93**
Max ^{o}F		0.91**	0.57**
Min ^{o}F			0.72**

Data on cob length, an important yield component, were also subjected to the regression analyses using the four climatic factors which were means over the three month period. Positive correlation between cob length and each of the climatic factors were obtained in all the hybrids (Table 60). Highly significant correlation was obtained with solar radiation, minimum temperature and daylength in all the hybrids. In the case of maximum temperature, the correlation coefficient was non-significant except H816.

In most of the hybrids, daylength was found to be the most important climatic factor affecting cob length (Table 61), and the longer the daylength the longer the ear. However, in H787, solar radiation was the most important with a positive b_i. Although, the correlation coefficients between cob length and solar radiation was almost as high as that with daylength, the solar radiation variable did not enter into the equation. This may be due to the high correlation between these two climatic variables and since solar radiation was entered after daylength, the estimation of its effects was reduced. The hybrid H763 was the only hybrid in which solar radiation, maximum temperature and daylength had significant effects on cob length. The b_i for maximum temperature was negative suggesting that high maximum temperature tend to favor faster development leading to shorter cob length. However its correlation with cob length was positive although not significant. The multiple correlation was again highly significant.

Grain yield was also analyzed in relation to these four climatic factors which were means over the three months. The correlation coefficients between grain yield and each of the climatic factors are shown in Table 62. Grain yield was positively and significantly

Table 60. Correlation coefficients between cob length and several climatic factors for the 6 hybrids

	H652	H763	H787	H814	H815	H816
Langleys/day	0.82**	0.88**	0.86**	0.76**	0.81**	0.84**
Max °F	0.48	0.38	0.40	0.46	0.43	0.57**
Min °F	0.62**	0.58**	0.63**	0.65**	0.58**	0.65**
Daylength	0.86**	0.90**	0.84**	0.78**	0.86**	0.89**

Table 61. Partial regression coefficients between cob length and several climatic factors for the 6 hybrids

	H652	H763	H787	H814	H815	H816
Langleys/day	--[a]	0.014	0.033	--	--	--
Max °F	--	-0.316	--	--	--	--
Min °F	--	--	--	--	--	--
Daylength	2.701	2.082	--	3.648	2.295	2.432
Constant	-16.079	12.672	2.790	-29.752	-12.357	-13.733
Multiple R	0.86**	0.92**	0.86**	0.78**	0.86**	0.89**

[a] not selected

Table 62. Correlation coefficients between grain yield and several climatic factors for the 6 hybrids

	H652	H763	H787	H814	H815	H816
Langleys/day	0.63**	0.71**	0.73**	0.78**	0.75**	0.71**
Max °F	0.48	0.27	0.35	0.53*	0.40	0.60**
Min °F	0.51*	0.43	0.53*	0.71**	0.49*	0.60**
Daylength	0.70**	0.79**	0.79**	0.80**	0.82**	0.78**

correlated with solar radiation and with daylength. In the case of maximum and minimum temperature, correlation was positive but was significant only in H814 and H816 for maximum temperature and significant in most hybrids for minimum temperature.

The partial regression coefficients shown in Table 63 indicated that daylength was important in affecting grain yield in corn. The longer the duration of light, the higher the yield. Solar radiation did not enter the equation for the reason already mentioned earlier, although its correlation with yield was almost as high as the correlation between daylength and yield. Maximum temperature was also important in affecting yield in H763. The negative b_i for day or maximum temperature suggested that the higher the temperature, the lower the yield. From this result, it appeared that H763 would yield very well under long days but cool temperature. Although the b_i for maximum temperature was negative, the correlation between this climatic factor and grain yield was positive but non-significant. The multiple correlation was also highly significant in all the hybrids.

The inclusion of all the climatic factors would not give a clear relationship of each of these variables to grain yield. Since solar radiation is a major factor in crop production but did not appear to be an important variable as a result of the high correlation with light duration, a separate analysis of solar radiation and yield was made. Three monthly means of solar radiation were used as the independent variables with grain yield as the dependent variable. The first month solar radiation mean has its effect on the vegetative phase (i.e. pre-tassel initiation) of the corn plant in relation to grain yield.

Table 63. Partial regression coefficients between grain yield and several climatic factors for the 6 hybrids

	H652	H763	H787	H814	H815	H816
Langleys/day	--[a]	--	--	--	--	--
Max °F	--	7.618	--	--	--	--
Min °F	--	--	--	--	--	--
Daylength	37.006	63.165	38.394	45.628	38.320	48.786
Constant	-299.063	18.287	-128.825	-459.829	-334.424	-440.990
Multiple R	0.70**	0.82**	0.80**	0.80**	0.82**	0.78**

[a] not selected

The second month solar radiation mean was related to the reproductive phase of the crop plant (i.e. from tassel initiation to silking). The grain filling period would be related to the third month solar radiation mean. The correlation between grain yield and each of the three monthly solar radiation means are shown in Table 64. The correlation coefficients between grain yield and the second and also the third months of solar radiation were positive and highly significant in all the hybrids studied. In the case of the first month, significance in the correlation with yield was found in H814, H815 and H816.

Solar radiation in the third month of the plant's growth corresponding to the grain filling period was found to have an important effect on grain yield in most hybrids except H816 (Table 65). In H814, all the three months were important in contributing to grain yield, while in H815, the second and the third months were important. Nevertheless, the third month was the most important as indicated by the large b_i. The second month of solar radiation corresponding to the period of ear shoot development was most important in affecting grain yield in H816. The multiple correlation was highly significant in all hybrids. The data here showed that solar radiation was important, but did not appear in the equations of Table 63 because solar radiation and daylength was highly correlated.

In view of the high correlation between daylength and solar radiation, the daylength variable was excluded for a separate analysis. In this analysis, additional variables were included. These were the first, second and the third monthly solar radiation means, and the mean solar radiation of the first two month period. The correlation coefficients between grain yield and these climatic variables are shown in Table 66.

Table 64. Correlation coefficients between grain yield and monthly solar radiation means for the 6 hybrids

Langleys/day	H652	H763	H787	H814	H815	H816
1st month	0.38	0.40	0.37	0.62**	0.47*	0.58**
2nd month	0.60**	0.66**	0.68**	0.70**	0.69**	0.66**
3rd month	0.62**	0.73**	0.79**	0.70**	0.75**	0.57**

Table 65. Partial regression coefficients between grain yield and monthly solar radiation means for the 6 hybrids

Langleys/day	H652	H763	H787	H814	H815	H816
1st month	--[a]	--	--	0.192	--	--
2nd month	--	--	--	0.061	0.130	0.365
3rd month	0.283	0.422	0.298	0.233	0.214	--
Constant	37.890	4.956	-8.777	-93.107	-3.576	9.552
Multiple R	0.62**	0.73**	0.79**	0.79**	0.78**	0.66**

[a] not selected

Table 66. Correlation coefficients between grain yield and some additional climatic variables for the 6 hybrids

	H652	H763	H787	H814	H815	H816
1st month langleys/day	0.38	0.40	0.37	0.62**	0.47	0.58**
2nd month langleys/day	0.60**	0.66**	0.68**	0.70**	0.69**	0.66**
3rd month langleys/day	0.62**	0.73**	0.79**	0.70**	0.75**	0.57**
Mean langleys/day (1st & 2nd)	0.54*	0.58**	0.58**	0.72**	0.64**	0.68**
Mean langleys/day (1st & 2nd & 3rd)	0.63**	0.71**	0.73**	0.78**	0.75**	0.71**
Max ^{o}F	0.48	0.27	0.35	0.53*	0.40	0.60**
Min ^{o}F	0.51*	0.43	0.53*	0.71**	0.49*	0.60**

The partial regression coefficients for this separate analysis are listed in Table 67. Hybrids H652 and H814 indicated that the average of the three months solar radiation was important in affecting grain yield. In H763 and H787, the solar radiation for the third month had the greatest effects on yield. In the other two hybrids, H815 and H816, solar radiation was again included in the regression equations in combination with temperature. This again demonstrated that solar radiation was important in affecting yield contrary to the analysis when daylength was included.

8.3 Discussion

Planting date experiments are important to assess the most suitable time of planting in the Corn Belt in view of its short growing season. Similarly such data are also important in the tropics although corn can be planted throughout the year. The monthly plantings in this study served to screen the best period of the year in which corn could be produced with high yields.

The average yield data in 1976 showed that plantings made in the period from April through August produced high yields as compared to the other months. This was related to the fact that corn planted during this period was exposed to longer and brighter days. Pendleton and Egli (1969) had suggested that early planting in the Corn Belt resulted in higher grain yields because the grain formation period occurred when the days were longer and brighter. The multiple regression analysis in this study also indicated that generally the longer the light duration the higher the grain yield, and that high light intensity during the third month (or grain filling period) was most important in contributing

Table 67. Partial regression coefficients between grain yield and some additional climatic variables for the 6 hybrids

	H652	H763	H787	H814	H815	H816
1st month langleys/day	--[a]	--	--	--	--	--
2nd month langleys/day	--	--	--	--	--	--
3rd month langleys/day	--	0.422	0.298	--	0.284	--
Mean langleys/day (1st & 2nd)	--	--	--	--	--	--
Mean langleys/day (1st & 2nd & 3rd)	0.353	--	--	0.472	--	0.694
Max ^{o}F	--	--	--	--	5.066	29.764
Min ^{o}F	--	--	--	--	--	-31.756
Constant	13.952	4.956	-8.777	-87.634	-388.774	-336.562
Multiple R	0.63**	0.73**	0.79**	0.78**	0.79**	0.82**

[a] not selected

to higher yield. The importance of radiation had also been shown by Scarsbrook and Dess (1973), and according to them there was a satisfactory fit of linear regression of grain yield on radiation.

Among the hybrids evaluated, H763 had the highest average yield for the twenty months. H763 is a single cross between Ant 2 (tropical) and B68 (temperate). Their genetic make-up might possibly provide strong buffering against climatic changes which resulted in a high average yield. The differential response obtained among the hybrids for these planting dates would suggest that it might be desirable to plant different hybrids for particular months.

In this study, days to mid-silk were greater in the winter months than in the summer. The six hybrids studied were single crosses involving temperate by temperate such as H787 (B68 x B37) and H814 (A632 x A619), temperate by tropical such as H652 (Oh545 x CM105) and H763 (B68 x Ant 2), and tropical by tropical such as H815 (CM111 x CM104) and H816 (Tx601 x CM111). Even though the hybrids were made up of different adaptation groups, their trends are more or less the same. Similar results were reported by Miller et al. (1968) for sorghum in Puerto Rico. They attributed the delay in flowering to delayed floral initiation caused by cool temperatures. The delay in flowering as studied here by the multiple regression analysis was found to be attributed to all the climatic factors studied, and not temperate alone. The fact that flowering occurred early in the long days of summer and late in the short days of winter indicates that photoperiod is not an important determinant of days to flowering for corn in the tropics. This would thus support the use of the term "neutral environment" in Hawaii or in the tropics (Brewbaker, 1974).

The monthly plantings in this study provided some valuable information on the effects of seasonal variation on grain yield. The highly significant interaction of hybrids by dates suggested that it is necessary to evaluate hybrids or varieties under different environments before any recommendations can be made for commercial plantings. Information can also be obtained for plant breeding purposes, if genetic materials like a diallel cross can be evaluated in a similar manner. This may then permit identification of inbreds or genotypes with good combining abilities for all seasons or for specific seasons.

9. CONCLUSION

Photoperiod sensitivity in corn has limited the exchange and use of germplasm among the different latitudes of the world. Photoperiod insensitive cultivars have been identified based on tassel initiation time in growth chamber studies under short- and long-day conditions. This laborious approach is not practical for plant breeding purposes, being time-consuming, destructive as well as limiting the number of lines screened at one time. Since there is a high correlation in Hawaii between the sensitivity difference of days to tassel initiation and leaf number as well as days to anthesis and silking, any of these three characters can be used instead.

A light set-up to extend daylength in the tropics is ideal for photoperiod studies since a control planting can also be made at the same time. Such light facilities will enable a larger number of cultivars or segregating progenies to be screened for photoperiod insensitivity under field conditions.

Leaf number measurements can be regarded as a better choice than days to anthesis and silking for studies on photoperiod sensitivity, mainly because leaf number is not as easily influenced by stress as flowering. On the other hand, it can be argued that for most practical purposes, if a high degree of accuracy is not required, days to anthesis may suffice. Days to silking is not preferred as silking delay always occur under different types of stresses as well as disease and insect infestations.

Genetic studies on photoperiod sensitivity should be independent of maturity effects for correct interpretation of results. Unfortunately, the generation mean studies carried out in this study had maturity

confounded with photoperiod sensitivity. Future studies should be conducted to partition out the maturity effects with the use of a control. Nevertheless, the genetical studies have indicated a comparatively simple inheritance for photoperiod sensitivity. As such, conventional methods of recurrent selection should be effective in converting sensitive tropical cultivars to low sensitivity.

The yielding potential of temperate by tropical crosses have been demonstrated in separate studies here. In addition, some of these temperate x tropical crosses tend to perform consistently well under the different seasons here in Hawaii.

Sensitivity to photoperiod may not be an advantage in temperate regions because of its late maturity, but it has a prospective yield potential under extended daylength studies in Hawaii. Some degree of photoperiod sensitivity should be retained to exploit this yield advantage especially for regions with intermediate daylengths, or even under the long days of the temperate regions if the delay in flowering is not too critical.

Low sensitivity to photoperiod as expressed in most temperate cultivars may likewise be converted to high sensitivity for possible use in the tropics. This approach may also be beneficial and warrants further study.

APPENDIX

Appendix 1. Average days to anthesis of CM104 x Tx601 exposed to different number of short days (SD) followed by long days

0 SD	10 SD	20 SD	30 SD	40 SD	50 SD	CSD
92.3	88.7	94.1	73.5	62.2	60.8	61.3

Mean Square = 699.85**

BLSD (0.05) = 4.9

Appendix 2. Average days to anthesis of CM104 x Tx601 exposed to different number of long days (LD) followed by short days

0 LD	10 LD	20 LD	30 LD	40 LD	50 LD	60 LD	70 LD	80 LD	90 LD	CLD
59.6	60.2	62.1	65.8	72.6	77.5	84.3	87.3	90.3	90.6	93.7

Mean Square = 524.06**

BLSD (0.05) = 3.8

Appendix 3. Mean values of plant characters in the 10 x 10 diallel cross under normal and extended daylength

Genotypes	Plant height (cm)		Ear height (cm)	
	ND	ED	ND	ED
Va35	197.9	200.9	66.9	65.1
A619	181.9	177.2	52.2	45.2
B37	190.8	199.6	78.1	80.8
Oh43	166.8	190.3	60.6	73.1
M017	200.5	208.8	81.7	73.3
Hi25	190.5	194.0	75.5	71.2
Hi26	203.8	201.4	90.0	84.5
Hi30	217.7	274.1	85.3	120.9
CM104	219.9	283.0	117.1	171.3
Tx601	189.1	201.5	87.3	139.6
Va35 x A619	222.1	212.7	73.2	56.4
Va35 x B37	230.7	221.0	92.6	82.5
Va35 x Oh43	210.4	217.1	76.1	73.5
Va35 x Mo17	221.3	224.4	88.1	80.5
Va35 x Hi25	225.9	230.9	85.3	75.0
Va35 x Hi26	235.7	241.9	99.7	96.2
Va35 x Hi30	231.5	252.4	85.0	83.4
Va35 x CM104	232.8	272.4	114.9	134.5
Va35 x Tx601	247.2	283.1	107.4	111.7
A619 x B37	220.1	209.2	76.3	66.1
A619 x Oh43	184.7	173.4	64.4	45.3
A619 x Mo17	226.0	231.0	84.0	73.7
A619 x Hi25	222.9	230.1	77.3	74.4
A619 x Hi26	232.8	255.1	83.6	96.3
A619 x Hi30	229.7	246.6	82.1	80.5
A619 x CM104	234.5	283.3	108.3	123.1
A619 x Tx601	237.0	292.2	95.1	116.3
B37 x Oh43	216.6	223.9	82.1	89.8
B37 x Mo17	218.5	232.2	83.2	82.3
B37 x Hi25	218.0	232.4	87.7	90.4
B37 x Hi26	247.6	259.0	106.6	112.1
B37 x Hi30	231.5	263.6	96.9	111.5
B37 x CM104	230.7	268.8	117.5	135.8
B37 x Tx601	232.7	269.3	109.7	128.8
Oh43 x Mo17	210.4	225.4	80.6	79.3
Oh43 x Hi25	208.4	228.1	77.8	80.1
Oh43 x Hi26	238.6	258.1	91.9	108.5
Oh43 x Hi30	218.4	264.7	86.0	114.0
Oh43 x CM104	228.0	258.9	107.9	134.2
Oh43 x Tx601	223.0	253.8	92.6	120.3
Mo17 x Hi25	221.0	235.6	86.2	82.7
Mo17 x Hi26	239.0	251.8	96.3	99.1
Mo17 x Hi30	224.4	254.9	88.2	101.0
Mo17 x CM104	228.8	273.3	112.6	132.0

Appendix 3. (Continued) Mean values of plant characters in the 10 x 10 diallel cross under normal and extended daylength

Genotypes	Plant height (cm)		Ear height (cm)	
	ND	ED	ND	ED
Mo17 x Tx601	240.7	279.5	107.8	127.2
Hi25 x Hi26	226.7	235.5	99.5	103.1
Hi25 x Hi30	223.2	264.3	96.1	114.3
Hi25 x CM104	220.0	261.9	104.6	126.9
Hi25 x Tx601	247.2	291.9	105.8	128.5
Hi26 x Hi30	242.6	283.5	110.0	129.8
Hi26 x CM104	233.9	280.3	124.2	146.6
Hi26 x Tx601	244.7	297.8	113.3	147.1
Hi30 x CM104	237.1	283.3	115.1	143.7
Hi30 x Tx601	254.1	313.6	115.4	138.3
CM104 x Tx601	246.9	289.8	129.3	173.3
Average	222.8	246.2	93.0	103.2
Interaction BLSD (0.05)	16.6		11.0	

ND = Normal daylength

ED = Extended daylength

Appendix 4. Mean values of yield components in the 10 x 10 diallel cross under normal and extended daylength

Genotypes	Row no.		Kernels/ row		Ear wt. (gm)		100 kernel wt. (gm)		Kernel depth (cm)	
	ND	ED	ND	ED	ND	ED	ND	ED	ND	ED
Va35	12.5	12.8	22.2	20.5	78.6	59.1	20.7	20.6	1.00	0.91
A619	14.9	13.6	16.6	14.5	66.3	46.1	25.8	21.1	0.97	0.84
B37	12.0	11.8	20.7	17.6	70.5	60.5	34.1	25.6	0.92	0.94
Oh43	12.9	13.0	23.4	22.9	74.0	68.6	29.5	20.4	0.91	0.98
Mo17	12.3	11.7	35.0	32.7	95.6	110.4	22.1	24.1	0.99	0.96
Hi25	13.1	13.2	18.8	14.1	65.1	52.9	40.2	24.8	0.97	0.96
Hi26	14.1	14.3	28.0	27.7	119.8	85.2	29.6	18.8	1.04	0.93
Hi30	13.2	13.0	25.3	25.8	106.8	118.9	26.8	27.8	1.04	1.02
CM104	14.5	9.3	29.1	9.3	163.1	47.3	31.2	23.7	1.01	0.81
Tx601	12.8	0.2	16.0	0.3	72.9	5.3	27.5	8.8	1.07	0.32
Va35xA619	14.2	14.1	29.6	25.8	109.9	90.0	27.0	21.7	1.02	1.01
Va35xB37	13.9	13.3	33.1	26.6	155.4	109.5	32.8	25.8	1.12	1.05
Va35xOh43	12.6	12.8	30.1	32.1	101.5	82.8	29.8	19.2	0.94	0.91
Va35xMo17	13.2	13.2	39.0	35.1	154.6	139.2	29.7	25.9	1.08	1.06
Va35xHi25	13.9	14.5	32.7	34.3	145.3	178.1	34.1	31.4	1.06	1.08
Va35xHi26	14.1	13.9	32.5	28.2	140.1	103.4	36.6	23.4	1.00	1.00
Va35xHi30	14.3	14.5	34.6	37.4	163.4	184.7	21.1	29.7	1.06	1.12
Va35xCM104	15.3	16.6	35.1	37.7	199.6	239.2	28.3	30.9	1.08	1.10
Va35xTx601	13.9	14.0	41.0	42.1	230.4	192.5	30.0	25.9	1.16	1.07
A619xB37	13.9	13.5	27.4	23.4	153.1	132.5	36.8	33.2	1.10	1.02
A619xOh43	14.4	13.4	27.8	14.6	96.2	40.1	32.4	18.7	1.01	0.86
A619xMo17	14.2	13.2	36.0	36.1	168.1	159.2	23.8	30.2	1.09	1.07
A619xHi25	15.5	14.8	25.2	29.2	134.8	143.0	30.6	27.9	1.06	1.07
A619xHi26	15.6	15.4	35.9	35.3	191.7	167.1	31.6	25.8	1.10	1.08
A619xHi30	15.9	16.0	33.5	37.8	173.9	202.9	33.8	30.0	1.17	1.14
A619xCM104	15.2	16.2	33.6	40.1	208.9	258.6	33.0	32.7	1.11	1.12
A619xTx601	14.9	15.5	38.3	43.7	275.3	262.5	26.4	33.6	1.19	1.17
B37xOh43	13.2	13.9	35.2	31.3	144.6	128.9	32.2	27.1	1.06	1.03
B37xMo17	12.4	12.6	39.2	37.2	152.8	142.7	34.2	27.2	1.10	1.03
B37xHi25	13.6	13.6	28.3	29.4	125.2	120.7	23.4	25.5	1.07	1.04
B37xHi26	12.9	12.8	37.6	41.0	186.8	182.7	24.9	28.8	1.07	1.09
B37xHi30	13.3	13.5	37.6	37.4	198.2	170.6	30.4	29.1	1.13	1.07
B37xCM104	14.5	15.3	34.5	32.1	215.7	195.3	22.9	32.9	1.16	1.13
B37xTx601	13.8	14.6	39.5	42.0	226.2	205.8	27.4	27.5	1.13	1.12
Oh43xMo17	12.9	13.3	39.8	40.6	153.6	160.1	26.5	26.7	1.11	1.08
Oh43xHi25	14.1	13.2	32.0	31.3	177.1	148.1	29.5	31.8	1.19	1.08
Oh43xHi26	14.9	15.2	36.4	39.8	183.7	186.0	31.1	27.0	1.10	1.09
Oh43xHi30	13.8	15.1	35.7	44.3	176.9	224.1	34.6	27.7	1.16	1.16
Oh43xCM104	14.9	14.8	39.0	40.5	227.0	276.0	26.0	33.4	1.19	1.18
Oh43xTx601	14.4	15.1	36.8	40.8	217.7	244.4	34.3	27.8	1.24	1.11
Mo17xHi25	13.0	13.1	34.9	37.0	147.7	185.8	29.8	32.8	1.09	1.15
Mo17xHi26	13.1	14.3	45.8	46.0	204.4	205.0	29.8	28.0	1.14	1.09
Mo17xHi30	13.3	14.0	34.2	40.1	132.7	184.4	29.4	28.9	1.03	1.10
Mo17xCM104	13.5	13.7	37.9	38.0	209.7	237.5	30.2	34.5	1.16	1.12
Mo17xTx601	13.6	14.1	41.8	38.4	207.2	182.7	35.5	27.8	1.13	1.10

Appendix 4. (Continued) Mean values of yield components in the 10 x 10 diallel cross under normal and extended daylength

Genotypes	Row no.		Kernels/ row		Ear wt. (gm)		100 kernel wt. (gm)		Kernel depth (cm)	
	ND	ED	ND	ED	ND	ED	ND	ED	ND	ED
Hi25xHi26	14.1	14.6	31.3	33.1	162.5	165.6	25.9	28.8	1.13	1.16
Hi25xHi30	13.9	14.7	33.4	35.8	169.1	189.9	28.3	31.1	1.12	1.16
Hi25xCM104	15.5	15.4	35.5	34.9	211.3	212.0	29.2	30.1	1.17	1.11
Hi25xTx601	14.0	14.4	36.6	38.6	208.1	240.0	28.6	29.0	1.15	1.13
Hi26xHi30	14.0	15.0	37.3	40.0	203.9	236.4	33.6	33.1	1.09	1.16
Hi26xCM104	15.9	17.3	40.4	37.6	235.5	244.0	35.4	29.9	1.10	1.08
Hi26xTx601	12.7	14.8	39.7	44.6	218.3	247.7	35.4	29.8	1.12	1.15
Hi30xCM104	15.3	15.7	36.0	36.5	208.7	230.4	32.4	33.1	1.13	1.09
Hi30xTx601	14.3	14.1	36.9	40.0	214.6	242.4	35.1	30.9	1.18	1.17
CM104xTx601	14.5	10.7	36.0	13.1	213.8	61.4	34.3	19.8	1.18	0.96
Average	13.9	13.8	33.3	32.5	164.5	159.8	30.1	27.3	1.09	1.04
Interaction BLSD (0.05)	5.1		5.5		37.2		4.0		0.09	

ND = Normal daylength

ED = Extended daylength

Appendix 5. Estimates of SCA effects of photoperiod sensitivity expressed in days to anthesis and silking in a 10-entry diallel cross evaluated in Hawaii

	Hi25	B37	A619	Oh43	Mo17	Hi26	Hi30	CM104	Tx601
Va35	-1.33[a]	1.66	0.33	0.43	-0.42	2.71	1.24	-2.35	0.11
	-1.47	2.09	0.67	0.41	-0.85	3.10	1.40	-3.23	1.60
Hi25		-0.07	0.50	-0.84	0.32	0.78	2.71	-2.25	-0.29
		-0.39	-0.51	0.90	0.47	0.11	3.22	-3.71	-0.32
B37			-0.04	-0.04	-1.16	-0.40	0.90	1.41	-4.16
			-0.29	-0.15	-0.78	0.97	0.54	2.18	-4.56
A619				1.16	-1.69	0.14	1.50	0.35	-4.66
				2.43	-3.06	0.02	0.96	0.43	-5.38
Oh43					-1.22	0.61	-0.13	0.01	-3.02
					-2.12	0.96	-1.00	-0.60	-3.64
Mo17						0.89	0.09	0.30	-2.57
						-0.30	-0.23	1.40	-2.77
Hi26							-2.25	-2.17	-5.61
							-3.32	-2.38	-5.92
Hi30								-5.04	-0.38
								-5.44	1.69
CM104									-2.74
									-0.88

[a] Upper and lower values represent days to anthesis and silking respectively

S.E. $(s_{ij} - s_{ik})$ = 1.67
1.96

S.E. $(s_{ij} - s_{kl})$ = 1.59
1.87

Appendix 6. Estimates of SCA effects of photoperiod sensitivity expressed in days to anthesis and silking in a 10-entry diallel cross evaluated in Illinois

	Hi25	B37	A619	Oh43	Mo17	Hi26	Hi30	CM104	Tx601
Va35	-2.13[a]	-0.53	0.48	-0.84	0.79	2.22	-1.18	-3.86	3.17
	-2.64	0.53	0.39	0.02	1.30	2.88	-1.96	-4.65	3.11
Hi25		1.00	0.61	-1.01	1.12	1.26	0.55	-1.63	-2.59
		1.38	-0.16	-1.62	0.75	1.23	-0.61	-0.50	-2.84
B37			-0.68	-0.31	2.12	-0.74	-1.45	0.27	-2.89
			0.16	-0.85	1.32	0.71	-0.93	0.27	-3.07
A619				0.70	-3.47	-0.34	0.96	-1.52	2.41
				0.71	-2.82	-0.23	1.12	0.23	1.09
Oh43					0.91	-0.06	-2.57	-0.24	-0.31
					-3.48	0.10	-1.84	2.16	0.52
Mo17						0.07	-0.04	-0.51	0.92
						-0.02	1.23	0.64	1.50
Hi26							-0.70	-2.18	-1.94
							0.12	-2.18	-2.32
Hi30								3.01	2.45
								0.58	3.14
CM104									-5.83
									-5.15

[a] Upper and lower values represent days to anthesis and silking respectively

S.E. $(s_{ij} - s_{ik})$ = 1.83
1.87

S.E. $(s_{ij} = s_{kl})$ = 1.75
1.78

Appendix 7. Cob length (cm) of the 10-entry diallel at two seasonal plantings

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601	Array mean
Va35	9.1[a]	10.1	10.1	10.2	9.7	13.4	10.0	12.1	14.5	11.6	11.1
	12.7	14.7	15.8	14.1	17.6	16.9	16.3	16.5	18.1	18.0	16.1
A619		6.8	11.0	8.1	12.8	10.6	12.0	11.1	12.8	12.3	10.8
		11.7	15.4	13.6	17.8	15.8	16.6	15.9	18.0	19.2	15.9
B37			7.2	10.9	11.7	10.5	11.8	11.9	11.7	11.9	10.9
			12.5	16.6	17.7	15.6	17.1	18.1	17.3	18.0	16.4
Oh43				9.3	11.9	12.5	11.3	11.9	13.3	12.2	11.2
				13.0	17.4	16.8	16.1	16.2	18.2	17.1	15.9
Mo17					8.9	12.9	13.5	11.9	13.4	12.7	11.9
					15.3	17.5	19.1	15.8	18.1	18.0	17.4
Hi25						10.7	13.0	13.8	13.9	13.7	12.5
						13.6	16.4	17.0	18.4	17.5	16.6
Hi26							9.5	13.8	14.3	14.1	12.3
							14.2	17.7	18.9	17.1	17.0
Hi30								11.5	13.2	13.1	12.4
								13.5	17.5	16.8	16.5
CM104									10.8	14.6	13.2
									16.2	17.6	17.8
Tx601										10.2	12.6
										11.7	17.1

[a] Upper and lower values represent Winter, 1976 and Summer, 1977 respectively

BLSD (0.05) = 2.85 Mean heterosis % = 29.91

3.00 26.97

Appendix 8. Kernels per row of the 10-entry diallel at two seasonal plantings

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601	Array mean
Va35	17.3[a]	19.0	21.3	20.4	20.2	22.7	20.9	25.4	29.4	27.1	22.4
	22.2	29.6	33.1	30.1	39.0	32.7	32.5	34.6	35.1	41.0	33.0
A619		8.5	24.7	15.9	28.1	19.9	27.3	23.0	25.9	25.6	21.8
		16.6	27.4	27.8	36.0	25.2	35.9	33.5	33.6	38.3	30.4
B37			11.2	24.8	27.1	21.6	28.4	24.7	23.7	27.6	23.5
			20.7	35.2	39.2	28.3	37.6	37.6	34.5	39.5	33.3
Oh43				20.7	30.2	25.8	25.9	24.7	25.2	29.1	24.3
				23.4	39.8	32.0	36.4	35.7	39.0	36.8	33.6
Mo17					18.9	29.0	35.2	26.2	27.9	30.4	27.3
					35.0	34.9	45.8	34.2	37.9	41.8	38.4
Hi25						14.9	27.5	26.5	28.1	30.3	24.6
						18.8	31.3	33.4	35.5	36.6	30.9
Hi26							16.8	30.0	31.7	30.6	27.4
							28.0	37.3	40.4	39.7	36.5
Hi30								23.1	26.4	28.8	25.9
								25.3	36.0	36.9	34.4
CM104									16.6	28.9	26.4
									29.1	36.0	35.7
Tx601										16.2	27.5
										16.0	36.3

[a] Upper and lower values represent Winter, 1976 and Summer, 1977 respectively

BLSD (0.05) = 4.0 Mean heterosis % = 62.29

3.7 53.47

Appendix 9. 100 kernel weight (gm) of the 10-entry diallel at two seasonal plantings

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601	Array mean
Va35	17.0[a]	23.0	22.8	20.3	16.7	20.3	22.3	23.7	22.9	19.3	20.8
	23.4	24.9	30.4	22.9	27.4	29.5	26.5	29.5	31.1	34.6	28.0
A619		17.4	23.0	17.4	16.6	24.6	21.1	20.8	26.4	24.6	21.5
		26.0	34.3	22.1	29.8	29.8	29.4	30.2	35.5	40.2	30.2
B37			24.8	17.4	16.5	19.9	22.3	22.8	29.5	24.2	22.3
			25.9	28.3	29.2	28.6	29.6	33.6	35.4	35.4	31.1
Oh43				15.8	14.4	18.6	17.7	18.6	23.8	20.9	18.5
				20.7	27.0	32.8	29.8	29.7	34.1	36.6	28.4
Mo17					15.1	17.3	13.7	14.9	22.4	21.4	16.9
					21.1	28.3	30.0	25.8	36.8	32.4	28.8
Hi25						19.9	20.7	24.1	26.8	22.5	21.5
						23.8	30.6	31.6	33.8	33.0	30.2
Hi26							21.7	22.6	21.6	21.6	20.5
							26.4	34.1	32.2	34.2	30.3
Hi30								19.9	22.8	22.9	21.3
								26.8	32.4	35.1	30.9
CM104									24.2	26.6	24.7
									31.2	34.3	33.7
Tx601										20.2	22.4
										27.5	34.3

[a] Upper and lower values represent Winter, 1976 and Summer, 1977 respectively

BLSD (0.05) = 3.7 Mean heterosis % = 8.23

3.4 23.35

Appendix 10. Mean grain yield (metric tons/ha) of the 10-entry diallel crossover the two seasons

	Va35	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601
Va35	2.83	4.64	5.61	3.96	5.16	6.00	5.01	6.54	7.91	7.91
A619		2.12	6.16	3.28	6.33	5.19	7.23	6.40	8.28	9.42
B37			2.38	5.49	5.62	4.86	6.78	7.00	8.04	8.24
Oh43				2.76	5.72	6.64	6.54	6.48	8.50	8.09
Mo17					3.28	5.55	7.10	4.88	7.84	7.87
Hi25						2.49	6.12	6.94	8.41	7.22
Hi26							3.93	8.16	8.84	8.04
Hi30								4.22	7.92	8.04
CM104									5.59	8.25
Tx601										3.02

Appendix 11. Estimates of SCA effects of grain yield of the 10-entry diallel at two seasons

	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601
Va35	6.4[a]	- 0.1	- 2.4	- 9.4	19.5	- 8.2	14.2	19.3	1.4
	-14.0	21.4	-24.9	15.3	16.5	-15.9	14.9	15.6	50.2
A619		21.9	-21.2	15.1	- 0.8	17.8	- 1.7	21.0	16.2
		9.8	-36.7	22.2	2.2	24.4	18.5	18.4	78.3
B37			9.1	7.0	-16.5	4.8	3.1	11.5	14.0
			2.8	2.7	2.9	18.5	29.8	16.5	37.2
Oh43				7.8	10.4	0.1	0.4	11.4	16.8
				11.8	41.8	21.8	21.8	38.1	35.7
Mo17					3.5	3.1	-13.4	6.8	18.5
					5.6	30.3	-24.3	14.3	20.1
Hi25						6.4	15.5	18.4	9.8
						- 3.6	17.4	23.5	9.4
Hi26							24.7	13.7	9.2
							21.6	15.3	10.0
Hi30								- 2.4	6.4
								3.2	15.3
CM104									5.3
									-16.7

[a] Upper and lower values represent Winter, 1976 and Summer, 1977 respectively

S.E. $(s_{ij} - s_{ik})$ = 8.0 / 14.8 S.E. $(s_{ij} - s_{kl})$ = 7.6 / 14.1

Appendix 12. Estimates of SCA effects of cob length of the 10-entry diallel at two seasons

	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601
Va35	0.31[a]	0.21	-0.13	-1.30	1.83	-1.33	0.54	2.29	-0.05
	-0.34	0.30	-1.02	1.02	1.12	0.22	0.77	1.09	1.96
A619		1.54	-1.79	2.30	-0.51	1.10	0.01	1.02	1.11
		0.08	-1.31	1.41	0.27	0.74	0.49	1.27	3.44
B37			0.94	1.06	-0.78	0.77	0.68	-0.14	0.58
			1.20	0.78	-0.38	0.71	2.16	0.01	1.68
Oh43				0.86	0.85	-0.13	0.21	1.02	0.44
				0.89	1.19	0.12	0.61	1.32	1.12
Mo17					0.64	1.49	-0.40	0.51	0.33
					0.41	1.64	-1.24	-0.26	0.61
Hi25						0.35	0.86	0.40	0.73
						-0.20	0.86	0.94	0.97
Hi26							1.14	1.05	1.37
							1.15	1.00	0.24
Hi30								-0.34	0.14
								0.02	0.34
CM104									0.99
									-0.20

[a] Upper and lower values represent Winter, 1976 and Summer, 1977 respectively

S.E. $(s_{ij} - s_{ik})$ = 0.69 / 0.74

S.E. $(s_{ij} - s_{kl})$ = 0.66 / 0.71

Appendix 13. Estimates of SCA effects of kernels per row of the 10-entry diallel at two seasons

	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601
Va35	0.13[a]	0.96	-1.34	-3.96	1.15	-3.17	2.08	6.22	3.01
	1.25	2.03	-1.45	2.50	3.76	-1.88	2.14	1.33	7.81
A619		5.54	-4.62	5.13	-0.50	4.42	0.93	3.94	2.79
		-1.06	-1.18	2.13	-1.03	4.18	3.71	2.44	7.78
B37			2.56	2.48	-0.42	3.90	0.91	0.06	3.14
			3.46	2.55	-0.75	3.13	4.99	0.58	6.16
Oh43				4.21	2.35	-0.10	-0.45	0.13	3.18
				2.62	2.46	1.41	2.67	4.60	3.00
Mo17					3.16	6.85	-1.37	0.44	2.06
					0.48	5.89	-3.82	-1.42	3.12
Hi25						1.75	1.50	3.28	4.53
						-0.97	3.02	3.72	5.49
Hi26							2.52	4.36	2.38
							1.47	3.16	3.17
Hi30								-0.22	1.29
								0.72	2.33
CM104									1.57
									-0.04

[a] Upper and lower values represent Winter, 1976 and Summer, 1977 respectively

S.E. $(s_{ij} - s_{ik})$ = 2.12 / 1.99 S.E. $(s_{ij} - s_{kl})$ = 2.02 / 1.90

Appendix 14. Estimates of SCA effects of 100 kernel weight of the 10-entry diallel at two seasons

	A619	B37	Oh43	Mo17	Hi25	Hi26	Hi30	CM104	Tx601
Va35	2.28[a]	0.77	2.20	-0.02	-0.59	2.07	2.92	-1.06	-2.44
	-2.70	2.16	-2.69	1.44	2.16	-1.17	1.34	0.19	3.50
A619		0.39	-1.25	-0.64	3.16	0.26	-0.57	1.85	2.34
		3.98	-5.54	1.79	0.37	-0.26	-0.04	2.54	7.02
B37			-2.52	-2.08	-2.92	0.12	0.12	3.64	0.64
			-0.06	0.51	-1.47	-0.83	2.65	1.80	1.54
Oh43				-0.21	-0.22	-0.52	-0.08	1.94	1.20
				0.92	5.34	2.08	1.40	3.11	5.39
Mo17					-0.14	-3.11	-2.40	1.88	3.11
					0.54	1.88	-2.84	5.51	0.82
Hi25						-0.35	2.56	2.04	0.04
						1.13	1.61	1.09	0.04
Hi26							1.72	-2.52	-0.30
							3.82	-0.83	0.91
Hi30								-1.78	0.58
								-1.12	1.29
CM104									1.06
									-2.16

[a] Upper and lower values represent Winter, 1976 and Summer, 1977 respectively

S.E. $(s_{ij} - s_{ik})$ = 1.89 / 1.84 S.E. $(s_{ij} - s_{kl})$ = 1.80 / 1.75

Appendix 15. Tests of significance of hybrids for individual planting dates of several agronomic characters

Planting dates	Days to mid-silk	Plant ht.	Ear ht.	Cob length	Filled ear length	Row no.	Kernels per row	Ear wt.	Grain yield	100 kernel wt.	Kernel depth
Oct 14/75	**	ns	**	ns	ns	**	*	ns	ns	*	*
Nov 11/75	**	*	**	**	ns	ns	**	**	**	**	ns
Dec 9/75	**	ns	*	*	*	ns	*	**	**	ns	ns
Jan 13/76	**	ns	*	ns	ns	ns	*	ns	ns	**	ns
Feb 10/76	**	ns	**	ns	ns	ns	ns	ns	ns	*	**
Mar 9/76	**	ns	**	ns	ns	ns	ns	ns	ns	ns	ns
Apr 13/76	ns	ns	*	ns	ns	ns	*	*	*	ns	ns
May 11/76	**	**	**	ns	ns	ns	**	**	*	ns	ns
Jun 8/76	ns	ns	*	ns	ns	ns	*	*	*	ns	ns
Jul 13/76	*	**	**	ns	ns	ns	*	*	**	ns	**
Aug 10/76	ns	*	**	*	*	ns	**	**	**	*	**
Sept 14/76	**	ns	**	ns	ns	*	ns	ns	ns	*	**
Oct 14/76	ns	ns	**	ns	ns	ns	*	*	ns	ns	**
Nov 9/76	**	ns	ns	ns	ns	*	*	*	*	*	*
Dec 14/76	**	**	*	ns	*	ns	*	**	**	**	**
Jan 11/77	**	ns	*	**	**	ns	*	*	*	**	*
Feb 10/77	**	ns	**	**	**	**	**	**	**	ns	**
Mar 8/77	**	ns	**	**	**	**	**	**	**	**	ns
Apr 12/77	**	*	*	*	**	**	**	**	**	*	ns
May 16/77	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

ns - non-significant

Appendix 16. Grain yield (metric tons/ha) of the 6 hybrids evaluated in 20 monthly plantings

Planting dates	H652	H763	H787	H814	H815	H816	BLSD (0.05)	CV %
Oct 75	8.14	7.96	6.36	6.27	6.50	9.26	1.51	10.5
Nov 75	6.49	5.15	4.71	3.98	4.66	3.81	0.58	6.9
Dec 75	5.99	8.18	3.46	2.28	5.80	5.05	1.52	16.5
Jan 76	5.86	6.41	2.78	1.68	5.24	6.33	2.73	29.3
Feb 76	6.67	10.14	7.17	6.84	6.44	7.10	3.16	18.0
Mar 76	7.27	14.95	8.98	7.22	7.66	7.16	5.29	28.2
Apr 76	12.70	15.83	8.10	6.73	9.64	12.04	3.59	17.6
May 76	11.22	12.64	7.79	8.49	10.63	15.20	2.12	10.7
Jun 76	12.52	14.00	6.87	10.25	10.42	11.01	2.28	11.4
Jul 76	11.86	11.13	9.09	7.98	9.17	12.87	1.30	7.0
Aug 76	10.68	11.42	7.10	7.91	8.17	13.08	0.67	4.0
Sep 76	7.96	8.42	5.53	5.70	7.42	8.42	2.43	15.5
Oct 76	6.46	7.65	4.61	1.67	6.19	6.04	2.67	25.2
Nov 76	5.98	5.63	3.34	1.49	4.56	5.56	1.47	18.2
Dec 76	7.13	7.31	3.80	1.82	5.08	6.52	1.00	10.8
Jan 77	7.49	7.98	4.37	2.36	5.46	7.40	2.22	20.4
Feb 77	11.47	10.36	7.64	6.74	9.37	8.43	0.44	3.0
Mar 77	11.48	8.86	7.26	3.67	9.83	11.69	2.04	13.0
Apr 77	10.64	13.37	8.97	5.52	11.01	10.18	1.16	6.7
May 77	7.49	12.43	8.55	8.47	8.79	8.14	3.12	16.3

Interaction BLSD (0.05) = 2.48

Appendix 17. Cob length (cm) of the 6 hybrids evaluated in 20 monthly plantings

Planting dates	H652	H763	H787	H814	H815	H816
Oct 75	15.8	17.0	15.1	14.6	14.4	16.0
Nov 75	14.4	15.0	14.5	13.1	13.2	11.8
Dec 75	13.6	16.2	12.8	9.5	13.1	13.2
Jan 76	13.4	14.4	11.4	9.5	12.9	14.1
Feb 76	15.6	17.4	15.2	15.8	14.4	14.4
Mar 76	17.7	20.2	18.1	17.7	15.8	15.8
Apr 76	19.2	20.8	18.7	16.4	17.5	18.0
May 76	19.2	19.9	19.0	18.4	17.7	19.2
Jun 76	21.1	20.6	19.2	20.7	18.0	17.2
Jul 76	18.6	19.2	17.6	16.4	16.8	18.6
Aug 76	18.2	19.1	16.0	16.0	16.0	18.0
Sep 76	16.0	16.2	14.6	15.5	15.0	15.4
Oct 76	12.6	14.5	10.8	9.4	14.4	12.9
Nov 76	13.0	12.9	10.9	9.1	11.9	12.6
Dec 76	14.1	14.1	10.6	9.4	11.6	12.9
Jan 77	14.2	14.9	12.5	10.2	13.6	14.2
Feb 77	17.6	17.4	15.6	15.5	16.6	14.9
Mar 77	17.7	18.8	14.8	12.2	16.9	16.4
Apr 77	19.1	20.3	17.2	14.1	18.1	18.0
May 77	17.6	21.0	18.6	19.3	17.3	17.2

Interaction BLSD (0.05) = 4.4

Appendix 18. Row number of the 6 hybrids evaluated in 20 montly plantings

Planting dates	H652	H763	H787	H814	H815	H816
Oct 75	15.5	12.8	13.1	15.2	14.6	16.2
Nov 75	14.7	13.7	12.6	13.9	15.2	12.2
Dec 75	14.8	12.5	10.7	13.4	14.2	13.0
Jan 76	13.9	13.0	11.2	11.8	13.6	13.2
Feb 76	14.4	13.5	13.4	14.4	13.5	14.3
Mar 76	15.4	14.0	14.0	15.1	14.8	13.8
Apr 76	15.0	13.4	13.8	14.6	14.5	15.1
May 76	15.7	14.1	14.2	15.2	15.0	14.4
Jun 76	15.2	14.8	13.7	14.4	15.4	15.8
Jul 76	15.8	13.8	13.1	15.7	14.5	15.0
Aug 76	15.8	13.6	13.9	15.2	14.5	15.4
Sep 76	14.6	14.2	13.2	14.8	14.8	14.4
Oct 76	13.7	13.0	12.6	11.8	14.4	13.2
Nov 76	15.5	12.6	12.1	11.8	13.9	13.4
Dec 76	14.8	13.3	12.8	12.1	14.3	14.2
Jan 77	15.5	14.2	13.9	13.4	14.9	14.5
Feb 77	16.3	13.5	13.4	15.2	14.9	13.5
Mar 77	15.1	13.6	13.6	14.4	15.8	14.7
Apr 77	15.4	14.2	14.4	16.2	15.4	14.6
May 77	16.0	13.7	14.6	15.2	16.1	14.5

Interaction BLSD (0.05) = 2.4

Appendix 19. Kernels per row of the 6 hybrids evaluated in 20 monthly plantings

Planting dates	H652	H763	H787	H814	H815	H816
Oct 75	30.2	29.3	21.4	25.5	26.6	33.4
Nov 75	27.4	21.4	19.2	16.8	21.0	19.6
Dec 75	23.6	29.8	13.6	10.4	24.2	16.8
Jan 76	26.2	24.6	14.0	11.2	24.8	29.5
Feb 76	32.4	35.8	28.7	24.4	28.8	31.6
Mar 76	30.8	41.8	32.5	28.9	32.9	25.6
Apr 76	38.4	42.1	24.0	27.8	36.3	39.2
May 76	39.0	41.6	30.4	30.5	37.2	44.8
Jun 76	38.6	43.8	27.9	35.9	35.6	34.2
Jul 76	38.2	38.0	31.8	23.2	32.6	37.5
Aug 76	34.6	37.7	24.0	23.4	30.6	37.8
Sep 76	32.5	26.8	22.4	23.4	28.5	32.2
Oct 76	26.7	26.4	16.6	10.6	25.7	28.2
Nov 76	23.8	22.8	15.5	10.4	21.0	27.3
Dec 76	30.0	25.6	17.2	12.4	21.6	27.4
Jan 77	28.0	30.1	22.0	15.2	20.6	30.4
Feb 77	39.8	34.3	31.4	28.2	32.8	33.6
Mar 77	39.2	41.6	29.2	20.2	33.8	35.7
Apr 77	42.1	46.8	35.6	25.4	37.0	41.1
May 77	33.1	45.2	38.6	36.2	33.6	39.0

Interaction BLSD (0.05) = 7.9

Appendix 20. 100 kernel weight (gm) of the 6 hybrids evaluated in 20 monthly plantings

Planting dates	H652	H763	H787	H814	H815	H816
Oct 75	30.1	35.2	38.2	28.4	27.6	28.9
Nov 75	26.4	27.3	31.1	28.6	24.4	22.6
Dec 75	26.5	32.9	35.8	25.3	27.4	30.4
Jan 76	23.8	28.4	25.5	17.8	25.3	26.2
Feb 76	23.8	29.9	30.4	29.6	25.4	24.1
Mar 76	25.4	32.2	28.2	28.0	23.2	29.4
Apr 76	29.2	31.1	35.0	25.1	26.8	29.2
May 76	26.3	27.7	26.0	27.4	26.1	25.9
Jun 76	32.2	33.0	28.6	31.5	25.6	26.2
Jul 76	29.6	32.6	32.0	35.4	28.3	34.4
Aug 76	31.8	35.2	34.0	36.8	29.8	36.1
Sep 76	28.8	36.1	31.7	27.4	28.6	30.8
Oct 76	29.9	35.9	32.7	23.6	28.2	26.8
Nov 76	27.1	32.4	31.6	22.4	26.9	25.6
Dec 76	26.5	36.8	30.4	21.4	28.1	28.6
Jan 77	29.8	31.4	23.7	22.2	31.0	28.0
Feb 77	30.2	34.4	31.8	27.3	32.4	31.2
Mar 77	33.6	31.4	32.4	23.0	31.6	34.3
Apr 77	29.0	34.0	31.7	24.4	31.6	28.4
May 77	26.8	32.8	29.9	30.8	29.0	25.4

Interaction BLSD (0.05) = 5.1

Appendix 21. Kernel depth (cm) of the 6 hybrids evaluated in 20 monthly plantings

Planting dates	H652	H763	H787	H814	H815	H816
Oct 75	1.06	1.18	1.13	1.06	0.97	1.14
Nov 75	1.05	1.07	1.11	1.02	0.98	1.03
Dec 75	1.05	1.19	0.98	1.00	1.03	1.06
Jan 76	1.04	1.12	1.00	0.88	0.98	1.01
Feb 76	0.99	1.16	1.13	1.06	0.94	1.02
Mar 76	1.06	1.19	1.08	1.05	1.02	1.04
Apr 76	1.11	1.17	1.14	1.04	1.04	1.12
May 76	1.20	1.19	1.12	1.08	1.06	1.16
Jun 76	1.16	1.18	1.18	1.12	1.00	1.10
Jul 76	1.16	1.22	1.17	1.12	1.08	1.22
Aug 76	1.17	1.28	1.17	1.18	1.08	1.25
Sep 76	1.10	1.29	1.08	1.06	1.06	1.17
Oct 76	1.08	1.22	1.13	0.92	1.06	1.08
Nov 76	1.12	1.18	1.04	0.91	1.01	1.08
Dec 76	1.04	1.22	1.09	0.90	1.04	1.05
Jan 77	1.10	1.16	1.02	0.92	0.98	1.01
Feb 77	1.12	1.24	1.11	1.06	1.11	1.15
Mar 77	1.18	1.10	1.11	0.97	1.12	1.18
Apr 77	1.16	1.21	1.12	1.01	1.10	1.14
May 77	1.08	1.25	1.12	1.11	1.05	1.10

Interaction BLSD (0.05) = 0.11

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